JOSSELYN VAN TYNE MEMORIAL LIBRARY
WILSON ORNITHOLOGICAL SOCIETY

THE CONDOR

Volume 62 September-October, 1960 Number 5

JOURNAL OF THE COOPER ORNITHOLOGICAL SOCIETY

THE CONDOR

JOURNAL OF THE COOPER ORNITHOLOGICAL SOCIETY

Published bi-monthly at Berkeley, California. Entered as second-class matter at the postoffice at Berkeley, California, May 15, 1925, under Act of Congress of March 3, 1879. Issued from the office of THE CONDOR, Museum of Vertebrate Zoology, Berkeley 4, California.

MANUSCRIPTS

Send manuscripts for publication to the Editor, ALDEN H. MILLER, Museum of Vertebrate Zoology, Berkeley 4, California, or to one of the Associate Editors, JOHN DAVIS or FRANK A. PITELKA, same address. Refer to suggestions on preparation of manuscripts for THE CONDOR on the back cover of recent issues of the journal.

SUBSCRIPTION RATES

Subscription price to non-members, five dollars per volume, payable in advance. Single copies, one dollar each.

MEMBERSHIP DUES

Regular members, four dollars per year in the United States, of which three dollars are for a year's subscription to The Condor; four dollars and twenty-five cents per year in all other countries in the International Postal Union. Sustaining members, five dollars per year.

The life membership fee is one hundred dollars. No additional dues are required. The money is invested and the interest only is used for Society publications. Life members receive THE CONDOR without additional charge. Concerning memberships, address C. V. DUFF, 2911 Antelo View Drive, Los Angeles 24, California.

Send dues, subscriptions and notices of change of address to JACK C. VON BLOEKER, JR., Los Angeles City College, 855 N. Vermont Ave., Los Angeles 29, California.

Send orders for back numbers of THE CONDOR and the PACIFIC COAST AVIFAUNA series to THOMAS R. HOWELL, Department of Zoology, University of California, Los Angeles 24, California.

Issued September 23, 1960

CONTENTS

PAGE

Relation of Growth and Development to Temperature Regulation in Nestling Vesper Sparrows
William R. Dawson and *Francis C. Evans* 329

The Middle American Populations of the Crested Flycatcher *Myiarchus tyrannulus*.....*Wesley E. Lanyon* 341

Life History of the Cactus Wren. Part III: The Nesting Cycle.....*Anders H. Anderson* and *Anne Anderson* 351

The Whistling Swan in the West with Particular Reference to Great Salt Lake Valley, Utah.....*Glen A. Sherwood* 370

Agonistic Behavior in the House Finch. Part II: Factors in Aggressiveness and Sociality.....*William L. Thompson* 378

FROM FIELD AND STUDY

Speed of the Allen Hummingbird While Diving.....*Oliver P. Pearson* 403

Thyroid Activity in Nestling Vesper Sparrows.....*William R. Dawson* and *John M. Allen* 403

Black Rail in San Joaquin Valley of California.....*John R. Arnold* 405

Insects Available for a Mockingbird Wing-flashing in February.....*Jack P. Hailman* 405

Additional Data on the Establishment of the Chestnut-backed Chickadee at Berkeley, California
Keith L. Dixon 405

Notes on Winter and Early Spring Bird Activity on the Farallon Islands, California.....*Asa C. Thoresen* 408

Confirmation of Occurrence of the American Redstart in Coastal Santa Barbara County, California
Charles H. Richardson and *Alice I. Richardson* 408

Recent Records of the Little Owl and Water Rail in Korea.....*Chester M. Fennell* 409

Notes on the Behavior of the Xantus Hummingbird.....*Ira L. Wiggins* 409

Records of Lewis Woodpecker for Humboldt County, California.....*Charles F. Yocom* 410

Immature Wood Duck, a photograph.....*John L. Blackford* 411

NOTES AND NEWS..... 412

THE CONDOR

VOLUME 62 SEPTEMBER-OCTOBER, 1960 NUMBER 5

RELATION OF GROWTH AND DEVELOPMENT TO TEMPERATURE REGULATION IN NESTLING VESPER SPARROWS

By WILLIAM R. DAWSON and FRANCIS C. EVANS

Simultaneous measurements of growth, metabolism, and body temperature of young altricial birds have as yet been reported for only a few species, and further data are necessary before an adequate analysis can be made of the factors involved in the establishment of homeothermy, or constant high temperature, in these animals. We have therefore extended our previous study of nestling Field and Chipping sparrows, *Spizella pusilla* and *S. passerina* (Dawson and Evans, 1957) to include an investigation of the Vesper Sparrow, *Pooecetes gramineus gramineus*. In addition to studying the general growth and temperature regulation of nestlings of this species, we have also analyzed the growth rates of certain of their visceral organs.

ACKNOWLEDGMENTS

This study was supported in part by grants from the Horace H. Rackham School of Graduate Studies of The University of Michigan and from the National Science Foundation (G–2096). We are grateful for the assistance rendered by L. C. Binford, R. H. Brand, R. T. Calef, P. S. Martin, R. C. Root, and T. J. Rupp.

MATERIALS AND METHODS

The field observations reported in this study were made on the Edwin S. George Reserve of The University of Michigan, approximately 4.5 miles west of Pinckney, Livingston County, Michigan, from 1949 to 1957. The 46 nestlings studied in the laboratory were obtained in the breeding seasons of 1955, 1956, and 1957; most of them were from the Reserve, but a few were obtained in adjacent areas. The procedures for nestling inspection were the same as those used previously (Dawson and Evans, 1957).

Observations were made of body weight, developmental state, condition of the plumage, and behavior. As in Field and Chipping sparrows, removal of Vesper Sparrows from the nest for the few minutes required for examination did not appear to disturb the younger nestlings, but those about to fledge sometimes left the nest at the approach of the observer. It was therefore difficult to obtain information for the last day or so of the nestling period. We have also followed our earlier procedure with regard to age designation: young examined on the day of hatching were recorded as 0 days old.

Nestling Vesper Sparrows to be studied under experimental conditions were generally taken into the laboratory in the afternoon, with approximately an hour elapsing between removal from the nest and arrival at the laboratory. Weight losses in transit were rarely more than 0.5 gm. Upon entering the laboratory, all nestlings were fed meal worms (*Tenebrio* larvae) and crickets until replete. They were then subjected to experimental procedures for determination of the relation of oxygen consumption and body temperature to environmental temperature. Subsequently the birds were fed every 2 hours between experiments. This feeding schedule kept them in good condition throughout the period in which they were studied. All measurements were made within 12 hours of the removal of the birds from the nest.

Our methods for determining the effects of environmental temperature on oxygen consumption and on body temperature were similar to those we had used previously. During the experimental periods, the nestlings were kept in chambers fitted with ports for connection to an air line and with a housing for a thermometer. In the chambers, the birds rested on packing material shaped to simulate a nest. They were housed singly, except for very small nestlings which were placed two in a chamber and prevented from huddling by means of a partition.

Metabolic rate was measured as oxygen consumption, with a Beckman paramagnetic oxygen analyzer. Rate of air flow through the chambers was maintained constant in

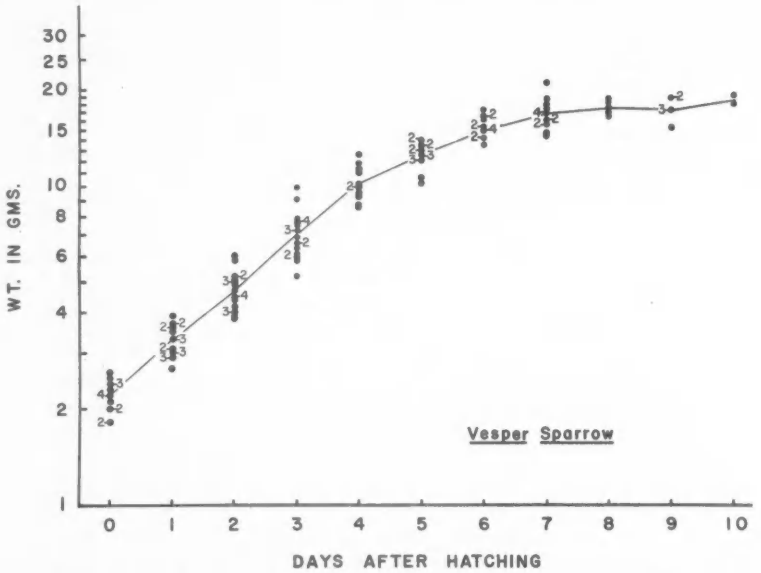

Fig. 1. Growth of nestling Vesper Sparrows plotted on a semi-logarithmic grid. The numerals indicate the number of individuals represented by the points which they accompany. The line connects the mean weights for successive ages.

each experiment but ranged from 100 to 350 cc/min. in the course of the investigation. All gas volumes specified in relation to metabolic rate have been corrected to O°C. and 760 mm. Hg. Body temperatures were measured rectally, either with a quick-registering thermometer designed for small-animal work or with fine (30 gauge) wire copper-constantan thermocouples sheathed in vinyl tubing and used in conjunction with a suitably calibrated recording potentiometer. The values presented for body temperature and oxygen consumption at various environmental temperatures are those observed at the end of the 2-hour experimental periods. Handling of the birds between removal from the chamber and determination of body temperature was kept at a minimum to avoid transfer of heat.

Temperature was maintained within 0.5°C. of the desired level during the experiments by placing the chambers in a 17 cubic foot constant temperature cabinet. Prior

to the initiation of each experiment, the birds were adjusted to room temperature (23° to 30°C.); in the experimental program they were exposed to constant temperatures between 10° and 40°C. When several experiments were run with the same bird, the initial one involved a warm environmental temperature (30° to 40°C.), the next a moderate temperature (20° to 30°C.), and the last a cool temperature (10° to 20°C.).

All young Vesper Sparrows studied in 1955 were sacrificed at the completion of the physiological measurements, and their thyroid glands were removed for histological study (see Dawson and Allen, 1960). Immediately after thyroid removal, the carcasses were tightly wrapped in aluminum foil and quick-frozen. They were later thawed and the liver and heart were carefully dissected out and weighed.

RESULTS

DURATION OF THE INCUBATION AND NESTLING PERIODS

The incubation period, defined as the interval between the date of laying of the last egg and the date of hatching of the last young when all eggs hatch (Nice, 1953), was observed throughout for 11 nests of the Vesper Sparrow; it was recorded as 12 days for 6 nests and as 13 days for 5 nests.

Table 1

Age at Fledging in the Vesper Sparrow

Age at leaving nest (days after hatching)	Number of individual records
7	3
8	4
9	32
10	46
11	10
12	1
Total records	96
Mean age on leaving nest	9.6 days

The length of the nestling period was recorded for 96 Vesper Sparows (table 1). The mean age on leaving the nest was 9.6 days, although some birds did not remain in the nest for more than 7 days and one stayed for 12 days. If the day of deposition of the last egg is taken as the beginning of development, the average age at fledging is approximately 22 days for the Vesper Sparrow. However, in this as well as in our previous study, we have followed the general practice of calculating the ages of nestlings from the day of hatching, as mentioned previously.

GROWTH DURING THE NESTLING PERIOD

Weights of 42 nestling Vesper Sparrows of known age were obtained; 34 birds were weighed on two or more days and two were weighed throughout the nestling period. Vesper Sparrows weigh about 2 gm. at hatching. They attain a weight of approximately 18 gm. before leaving the nest (fig. 1). However, despite this rapid growth, they achieve prior to fledging only about three-quarters of their mature weight—the mean weights of 15 adult female and of 28 male Vesper Sparrows taken in lower Michigan in spring and early summer (from the collections of The University of Michigan Museum of Zoology) were 24.9 and 26.5 gm., respectively.

The general pattern of nestling growth in the Vesper Sparrow is in most respects similar to that found in the Field and Chipping sparrows. Growth is relatively rapid during the first four days after hatching and slows thereafter. The values for the instan-

taneous percentage growth rate r (Brody, 1945:508) range from approximately 40 per cent in the early part of the nestling period to 5 per cent between the seventh and eighth days after hatching (table 2).

Table 2

Instantaneous Percentage Growth Rates (r) in Nestling Vesper Sparrows

Interval in days after hatching	r (per cent/day)
0–1	40.4
1–2	35.4
2–3	41.2
3–4	34.5
4–5	20.1
5–6	18.1
6–7	10.1
7–8	5.2

Records of heart and liver weight were obtained for 34 nestling Vesper Sparrows (figs. 2, 3). The essentially straight-line relationship between the weights of these organs and total body weight on a double logarithmic grid is described by the familiar equation for heterogonic growth,

$$D = a\ W^k$$

where D is organ weight, W is body weight, and a and k are constants, the latter indicating the slope (Huxley, 1932; Brody, 1945). The values of k for the lines fitted free-

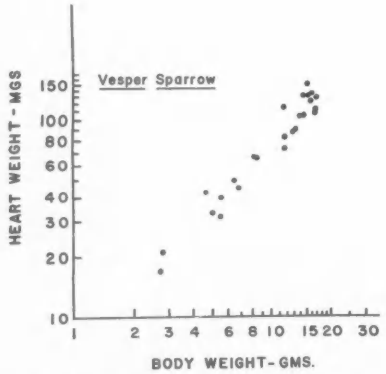

Fig. 2. The relation of heart weight of nestling Vesper Sparrows to body weight, plotted on a double logarithmic grid. The slope of the best line fitted free-hand to these points is 1.1.

hand to the data are 1.1 and 1.2 for heart and liver, respectively. The fact that the values exceed unity indicates that these organs grow relatively more rapidly during the nestling period than the body as a whole. This may well contribute to the increase of metabolism per unit of body weight evident during the nestling period (fig. 4). Com-

parable data on nestlings of other altricial species are not available, except for those summarized in Brody (1945) for the Rock Dove (*Columba livia*). In this latter species, the value of k for the relationship between heart and body weight declines from 1.8 to 1.0 during the first 9 days of post-hatching growth. The value of k for the relation between liver weight and body weight decreases from 1.6 to 1.1 in the same period.

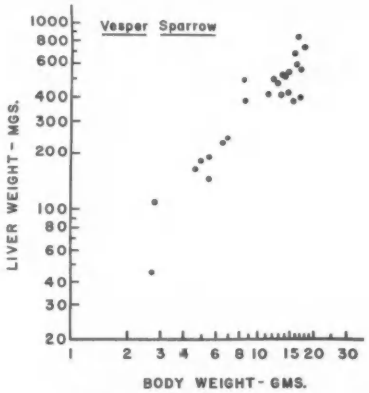

Fig. 3. The relation of liver weight of nestling Vesper Sparrows to body weight, plotted on double logarithmic grid. The slope of the best line fitted free-hand to these points is 1.2.

GENERAL DEVELOPMENT

Feathers.—The newly hatched Vesper Sparrow has a flesh-pink skin with patches of gray down on the capital, dorsal, humeral, femoral, secondary, and caudal tracts (Saunders, 1956). The pattern of feather development is similar to that of Field and Chipping sparrows and the Tree Sparrow, *Spizella arborea* (Baumgartner, 1938). The rate of growth of the feathers (table 3) is slower than those of the first two species and more rapid than that of the last. Unpigmented at first, the feather tracts of the Vesper Sparrows are clearly marked at 2 days of age, when the primaries have just emerged from their papillae. Extension of the feather sheaths occurs gradually; the rectrices emerge about the sixth day, when the primary quills are 10–12 mm. long and there is evidence of bursting sheaths, first seen in the feathers of the ventral tracts. By the eighth day, the lack of pigment in the outer rectrix is evident, in contrast to the dark quills of the other tail feathers. At 9 days of age the primary barbs have emerged 8 to 9 mm., the tail is 8 to 10 mm. long, and the birds appear well feathered and ready to leave the nest, although traces of down are still present and no feather is fully out of its sheath. Sutton (1941) observed that new feathers were emerging at either side of the ventral apterium in 13-day-old fledglings and that the rectrices continued growing until 31 days; the first signs of postjuvenal molt were noted by the eighteenth day.

Eyes.—As in Field and Chipping sparrows, the eyes of nestling Vesper Sparrows remain closed for the first few days after hatching. In some individuals, eyes began to open on the third day; in most they did not do so until the fourth or fifth day. The

ocular opening increased gradually and at 8 to 9 days of age was fully round. Like feather growth, eye development seems to take place a little more slowly in the Vesper Sparrow than in Field and Chipping sparrows.

Form and behavior.—Young Vesper Sparrows undergo a marked change in form while they are in the nest. At hatching the head is bent down, the legs are stretched forward, and the bird rests largely on its abdomen, which is conspicuously distended and remains so for the first few days. When upset a young bird rights itself only with

Table 3

Feather Development in Nestling Vesper Sparrows

Age (days) after hatching)	Sample size	Mean length of third primary sheath (mm.)	Mean length of exposed barbs of third primary (mm.)	Mean length of outer rectrix (mm.)
3	6	1.0	0	0
4	5	2.5	0	0
5	3	8.0	0	0
6	5	11.0	0	1.0
7	4	16.0	1.0	3.0
8	4	21.0	4.0	5.5
9	4	27.5	8.0	8.0
10	3	30.0	11.0	10.0

difficulty. At 6 days of age, the enlargement of pectoral and other muscles makes the abdomen less conspicuous. The legs now provide increased support, permitting the bird to stand. Movements are still awkward, however, and it is not until the eighth or ninth day that the nestling appears well coordinated.

Gaping was observed in Vesper Sparrows soon after they hatched, and it was the usual response to the presence of an observer at the nest as late as the sixth day. From the seventh day on, the birds typically assumed a crouching position and did not gape when the nest was disturbed. This change in reaction appears correlated with the completion of the opening of the eyes, as noted for the White-crowned Sparrow, *Zonotrichia leucophrys* (Banks, 1959).

OXYGEN CONSUMPTION

The relation of oxygen consumption to environmental temperature in Vesper Sparrows undergoes a pronounced change in the week following hatching (fig. 4). The oxygen consumption of birds 0 to 2 days old varied directly with temperature, with rates ranging in most cases from less than 0.5 cc/gm./hr. at 13° to 23°C. to 2–3 cc/gm./hr. at 35° to 38°C. A direct relation between temperature and metabolism was also evident in 3-day-old birds, but somewhat higher weight-relative rates of oxygen consumption than those observed in the younger individuals were maintained at all temperatures. The first suggestion of an inverse relation between oxygen consumption and environmental temperature was noted in 4-day-old Vesper Sparrows at temperatures between 20° and 35°C. In this range, metabolic rates were in excess of 3 cc/gm./hr. Below 20°C., oxygen consumption declined with decreasing temperature. Four-day-old Vesper Sparrows are apparently at a stage in the development of temperature regulation comparable to that achieved by Field Sparrows at 4 days, by Chipping Sparrows at 4 to 5 days, by House Wrens (*Troglodytes aedon*) at 6 days (Kendeigh, 1939), and by pigeons at 8 to 9 days (Pembrey, 1895) after hatching. On the fifth day, a few Vesper Sparrows increased their metabolism when exposed to environmental temperatures below 20°C., but this was not the characteristic response. A strictly inverse rela-

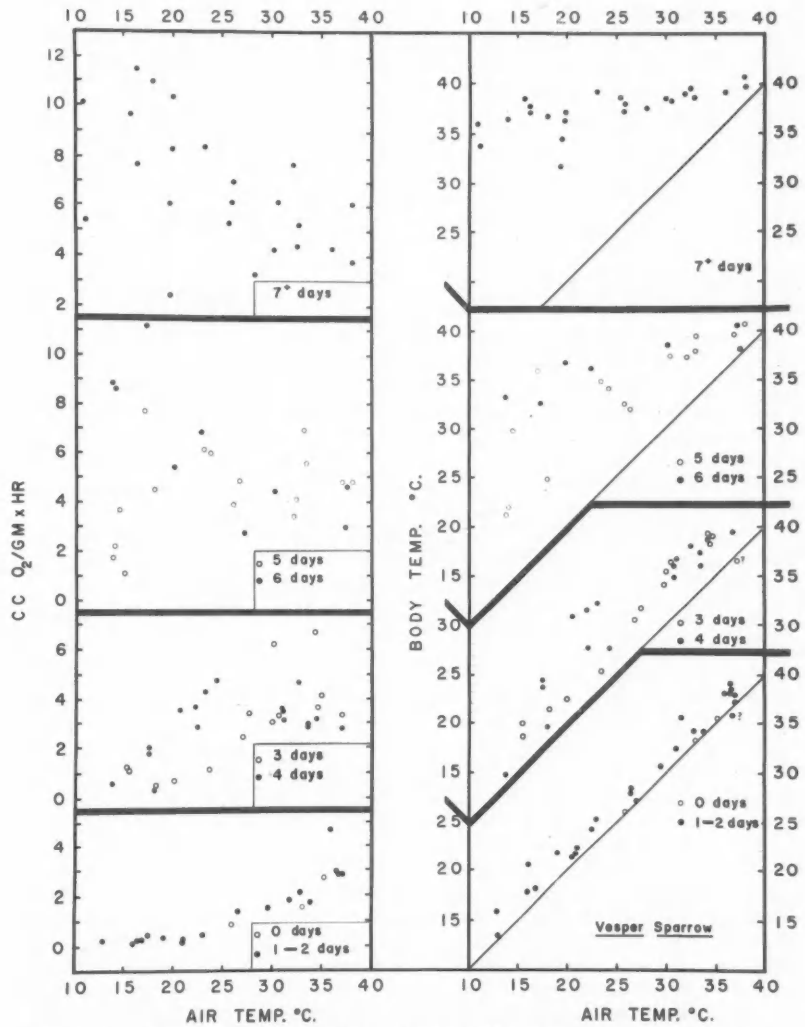

Fig. 4. The relation of oxygen consumption (left) and of body temperature (right) to environmental temperature. Oxygen consumption measured in cc/gm./hr.; temperature in degrees centigrade. All data obtained at the end of 2-hour experiments. Ages given as days after hatching. The uppermost graphs ("7+ days") summarize data for birds 7 to 9 days of age.

tion of metabolic rate to temperature was first evident on the sixth day. In the results for birds of 6 days or older, considerable scatter is evident, due most likely to variability in the activity of the birds in the course of the experiments. However, this does not obscure the basic relation between metabolism and temperature.

BODY TEMPERATURE

As suggested by the modification of metabolic response to temperature in the first few days after hatching, the nestling period is a time of rapid improvement in capacity for regulation of body temperature (fig. 4). Vesper Sparrows from 0 to 2 days old generally could not maintain body temperature more than 3°C. above environmental temperatures between 13° and 37°C. Some improvement was evident in 3-day-old birds, particularly at environmental temperatures from 28° to 35°C., and 4-day-old individuals successfully maintained body temperature as much as 10°C. above environmental temperatures between 20° and 25°C. Thermoregulatory capacity continued to improve on the fifth and sixth days after hatching, and at 7 to 9 days of age the birds were in most cases able to maintain body temperatures above 35° between environmental temperatures of 10° and 38°C.

The absence of effective temperature regulation in the younger nestlings resulted in their being chilled to relatively low body temperatures in the course of the experimental program, yet none of the birds tested appeared to suffer any ill effects, even when cooled to 13° to 20°C. for a period exceeding one hour. Additional observations were made to assess more fully the extent of the tolerance of 2-day-old Vesper Sparrows to chilling. Full recovery was made even when the birds were left at body temperatures of 18° to 20°C. for 8 hours. Tolerance of relatively low body temperatures by altricial nestlings has been noted previously in Field and Chipping sparrows, Horned Larks, *Eremophila alpestris* (Kelso, 1931), House Sparrows, *Passer domesticus* (Leichtentritt, 1919), and House Wrens (Baldwin and Kendeigh, 1932). Such tolerance is probably rarely required in nature, because of the effectiveness of parental brooding in maintaining body temperatures of the young at near-homeothermic levels.

DISCUSSION

In the Vesper Sparrow, as in other passerines for which information is available (see Dawson and Evans, 1957), the onset of homeothermy is not the culmination of any single aspect of development. It is linked with a complex array of processes which lead on the one hand to the establishment of functional neural mechanisms—sensory, integrative, and motor—controlling the various activities on which regulation of body temperature depends, and on the other hand to the development of capacities for heat conservation and to the improvement of abilities for heat production.

In the absence of direct information, we can say very little about the development in the Vesper Sparrow of the neural mechanisms on which homeothermy depends, except that they have started to function by the fourth day after hatching, when the first suggestion of an inverse relation between metabolism and oxygen consumption was noted (fig. 4). Similar observations were reported for Field and Chipping sparrows. Odum's (1942) report that the frequency of muscle tremors of 6-day-old House Wrens varied inversely with environmental temperature indicates at least partial function at this age of neural mechanisms responsible for regulation of heat production.

Newly hatched Vesper Sparrows possess little capacity for conserving heat, because of the relatively high proportion of their body surface to weight and because of their essentially naked condition. In the days following hatching, there is a progressive decline of the surface-weight relationship concomitant with increasing size; the values for this relationship (estimated by the formula $cm^2/gm. = 10\ gm.^{-0.33}$) for 6-day-old nestlings and for adult birds are, respectively, only 57 and 49 per cent of that for newly hatched young. The decline in the surface-weight relationship reduces heat loss of older nestlings per gm. of tissue and so assists in bringing it in line with the capacity for heat production.

The contribution of plumage development to the establishment of homeothermy in Vesper Sparrows is less clear cut, for effective regulation of body temperature at moderate (20° to 25°C.) environmental temperatures is evident when the contour feathers have just begun to erupt from their sheaths. A similar situation has been noted in the House Wren (Kendeigh, 1939), Rock Dove (Ginglinger and Kayser, 1929), and Field and Chipping sparrows (Dawson and Evans, 1957). These observations suggest that the development of an insulating plumage, although undoubtedly of importance in resistance to cold, is not requisite for the establishment of homeothermy at moderate environmental temperatures.

The capacities of newly hatched Vesper Sparrows for producing heat seem relatively restricted, probably owing primarily to the limited development of the muscular system and the rudimentary motor coordination at this age. These hatchlings are relatively passive creatures, whose awkward attempts at activity occur principally during feeding periods. In the first week after hatching, capacity for heat production increases concomitantly with the development of the musculature and increased motor activity. The relatively rapid growth of such organs as the heart and liver (figs. 2, 3) and the relatively high level of thyroid activity which seems to exist in nestlings from 2 to 6 days of age (see Dawson and Allen, 1960) may also serve to intensify heat production, which apparently reaches a level commensurate with homeothermy only during the latter portion of the nestling period (see fig. 4 in Dawson and Evans, 1957).

The various processes contributing to the establishment of homeothermy seem to proceed more rapidly in the Vesper Sparrow than in any other altricial bird thus far studied, with the exception of Field and Chipping sparrows. These three fringillids show effective temperature regulation at moderate environmental temperatures, that is, the maintenance of body temperature above 37°C. in an environment at 20° to 25°C., by 6 to 7 days after hatching. This compares with 8 days for the House Wren (Baldwin and Kendeigh, 1932), 7 to 8 days for the Red-backed Shrike (*Lanius collurio*), 10 days for parakeets (*Melopsittacus undulatus*) and 11 days for the Wryneck, *Jynx torquilla* (Boni, 1942), and 11 days for the Rock Dove (Ginglinger and Kayser, 1929). The three species of sparrows fledge in 10 days or less, whereas the House Wren does not do so until it is 15 days old. The speed with which homeothermy is established thus appears to correlate with the general pattern of development.

There is general agreement that the altricial condition is of particular biological significance from the standpoint of energetics (Kendeigh, 1952; Witschi, 1956; Dawson and Evans, 1957). The immature state of newly hatched altricial young and the relatively short period between fertilization and hatching do not require an egg so large or with an energy content as great as that needed in the precocial mode of development. Reduction in egg size and energy content may have been key developments in the evolution of very small birds (Witschi, 1956).

Another reason for the energetic significance of the altricial condition is that it minimizes the maintenance costs of the young during a major part of their development. The extensive brooding of the young by the parents during the early part of the nestling period maintains them in a relatively constant environment, even in quite cool surroundings (Irving and Krog, 1956). This is apparently accomplished at a trifling energetic cost to the parent birds, for they would have expended much of the heat which they impart to the young in their own temperature regulation even if they were not brooding. During the later stages of the nestling period, when brooding is less frequent, the young can still be well protected from excessive heat loss by huddling with their siblings and by the insulation afforded by the nest. Their maintenance costs are further reduced by parental feeding during the nestling period and for some time

after fledging. It is of particular interest that the metabolic rates (per unit of weight) of passerine nestlings that have been studied to date, including the Vesper Sparrow, do not, under conditions approximating those in the nest, rise to levels expected of homeotherms of comparable size until the approach of fledging (Dawson and Evans, 1957: fig. 4).

From the considerations outlined above, we conclude that the low maintenance costs of the sedentary and well-protected young of altricial birds should contribute to rapid and efficient growth. The extremely rapid growth of altricial nestlings is attested to by the statistics on instantaneous percentage growth rates provided in this and earlier studies (Dawson and Evans, 1957; Banks, 1959). A provisional consideration of growth efficiency can be made from an estimate based on data for the Vesper Sparrow. In this estimate, which is concerned with the early part of the nestling period when the young are generally inactive, the following assumptions are made: body temperature of young is 35°C.; 1 gm. of sparrow is equivalent to 2000 cal., based on data for the domestic fowl, *Gallus gallus* (Brody, 1945:53); and the caloric equivalent for oxygen is 4.8 cal. per cc consumed. The following data are used: metabolic rate of 0-, 1-, and 2-day-old Vesper Sparrows in a post-absorptive state at 35°C. is 2.5 cc O_2/gm./hr. (fig. 4), or 288 cal./gm./day; weight increments between 0 and 1 and between 1 and 2 days are 1.1 and 1.4 gm., respectively (fig. 1); and the geometric means of weight between 0 and 1 and between 1 and 2 days are 2.7 and 3.9 gm., respectively. Efficiency (E) can be calculated from the following equation:

$$E = \frac{(a)(100)}{(a+b)}$$

where a represents the calories accumulated in growth during the period considered and b represents the calories expended in metabolism (equivalent to the product of the geometric mean of weight and the cal./gm./day) during the same period. The denominator $(a+b)$ of this equation corresponds to the *net energy* expression of Brody (1945:34), that is, the difference between the gross (combustible) energy of the food ingested and the energy lost in the feces and excretory products plus the energy represented in specific dynamic action (SDA). In other words, the net energy equals the metabolizable energy increment of the food less the energy represented in SDA. Since b includes the energetic cost of maintenance, E represents a gross efficiency of growth. These specifications, although tedious, are necessary, since expressions of efficiency are ambiguous without them (Brody, 1945:54).

With respect to the net energy increment of the food ingested in the 24 hours after hatching, the gross efficiency of growth of Vesper Sparrows equals

$$\frac{(1.1)(2000)(100)}{(288)(2.7)+(1.1)(2000)}$$

or 74 per cent between 0 and 1 day after hatching. It equals 71 per cent for the interval between 1 and 2 days after hatching. These values seem quite high even though they are calculated with respect to the net energy increment of food. They may profitably be compared with estimates of gross efficiency for a precocial species, the domestic fowl, as summarized in Brody (1945:53). When the latter efficiencies are converted to a *net energy* increment basis (a conservative estimate is that net energy = 70 per cent of metabolizable energy) they are at least 10 per cent less than those calculated for the Vesper Sparrow. This provides further support for the conclusion that the altricial mode of development favors efficient growth.

SUMMARY

Observations on the growth and development of nestling Vesper Sparrows (*Pooecetes gramineus gramineus*) were made at the Edwin S. George Reserve, Pinckney, Michigan. Forty-six nestlings of various ages were used in the laboratory to establish the relations of oxygen consumption and body temperature to environmental temperatures. Growth rates of the heart and of the liver were also determined.

The incubation period, observed completely for 11 nests, was 12 to 13 days, and the mean length of the nestling stage for 96 young was 9.6 days. All ages subsequently specified indicate days after hatching. The young weighed about 2 gm. at hatching and attained a weight of approximately 18 gm. before leaving the nest. Growth was comparatively rapid during the first four days after hatching but slowed thereafter; liver and heart increased in weight relatively more rapidly than the body as a whole during the nestling period.

Feather tracts were clearly marked at 2 days of age when the primaries had just emerged. Rupture of feather sheaths and emergence of the rectrices occurred at 6 to 7 days, and the birds appeared well feathered at age 9 days. The eyes began to open at 3 to 5 days and the ocular opening was fully round at 8 to 9 days. Gradual muscular development permitted the young to stand when they were 6 days old, but well coordinated movement was not achieved until the eighth day after hatching. On approach of an observer the nestlings would gape during the first six days after hatching. Crouching replaced this response in older nestlings.

The oxygen consumption of birds 0 to 2 days old varied directly with environmental temperatures from 13° to 38°C. The first indication of an inverse relationship between oxygen consumption and environmental temperature was observed in 4-day-old birds at temperatures between 20° and 35°C. and was clearly evident at 6 days of age.

Nestlings from 0 to 2 days old were generally unable to maintain body temperature more than 3°C. above environmental temperatures between 13° and 37°C. Four-day-old individuals maintained body temperatures as much as 10°C. above environmental temperatures between 20° and 25°C. At 7 to 9 days of age most birds were able to keep their body temperature above 35°C. in environments between 10° and 38°C. Young nestlings showed considerable tolerance to chilling: 2-day-old birds recovered fully after being kept at body temperature of 18° to 20°C. for 8 hours.

The onset of homeothermy is linked with a complex array of processes leading to the establishment of functional neural control of body temperature regulation and to the development of capacities for heat production and conservation. Heat loss is reduced during the nestling period by a decline in the proportion of body surface to weight and probably also by feather development, although body temperatures were effectively regulated at moderate environmental temperatures even when the contour feathers had just begun to erupt from their sheaths.

The immature state of newly hatched young and the relatively short period between oviposition and hatching in altricial species do not require an egg as large or with as great an energy content as that needed in precocial species. The altricial condition also minimizes the maintenance costs of the young during a major part of their development, through parental brooding and feeding.

Based on the net energy increment of food ingested in the 24 hours after hatching, the gross efficiency of growth was estimated to be 74 per cent for the interval between 0 and 1 day after hatching, and 71 per cent for the succeeding 24-hour period. These high values support the conclusion that the altricial mode of development favors highly efficient growth.

LITERATURE CITED

Baldwin, S. P., and Kendeigh, S. C.
1932. Physiology of the temperature of birds. Scientific Publ., Cleveland Mus. Nat. Hist., 3:x+1–196.
Banks, R. C.
1959. Development of nestling white-crowned sparrows in central coastal California. Condor, 61:96–109.
Baumgartner, A. M.
1938. A study of development of young tree sparrows at Churchill, Manitoba. Bird-Banding, 9:69–79.
Boni, A.
1942. Ueber die Entwicklung der Temperaturregulation bei verschiedenen Nesthockern. Schweiz. Arch. für Ornith., 2:1–58.
Brody, S.
1945. Bioenergetics and growth (Reinhold Publ. Corp., N. Y.).
Dawson, W. R., and Allen, J. M.
1960. Thyroid activity in nestling vesper sparrows. Condor, 62:403–405.
Dawson, W. R., and Evans, F. C.
1957. Relation of growth and development to temperature regulation in nestling field and chipping sparrows. Physiol. Zool., 30:315–327.
Ginglinger, A., and Kayser, C.
1929. Etablissement de la thermorégulation chez les homéothermes au cours du développement. Ann. Physiol. et Physicochim. Biol., 5:710–758.
Huxley, J. S.
1932. Problems of relative growth (Methuen and Co. Ltd., London).
Irving, L., and Krog, J.
1956. Temperature during the development of birds in arctic nests. Physiol. Zool., 29:195–205.
Kelso, L.
1931. Some notes on young desert horned larks. Condor, 33:60–65.
Kendeigh, S. C.
1939. The relation of metabolism to the development of temperature regulation in birds. Jour. Exper. Zool., 82:419–438.
1952. Parental care and its evolution in birds. Illinois Biol. Monog., 22:1–356.
Leichtentritt, B.
1919. Die Wärmeregulation neugeborener Säugetiere und Vögel. Zeitschr. für Biol., 69:545–563.
Nice, M. M.
1953. The question of ten-day incubation periods. Wilson Bull., 65:81–93.
Odum, E. P.
1942. Muscle tremors and the development of temperature regulation in birds. Amer. Jour. Physiol., 136:618–622.
Pembrey, M. S.
1895. The effect of variations in external temperature upon the output of carbonic acid and the temperature of young animals. Jour. Physiol., 18:363–379.
Saunders, A. A.
1956. Descriptions of newly-hatched passerine birds. Bird-Banding, 27:121–128.
Sutton, G. M.
1941. The juvenal plumage and postjuvenal molt of the vesper sparrow. Occas. Papers Mus. Zool., Univ. Mich., 445:1–11.
Witschi, E.
1956. Development of vertebrates (W. B. Saunders Co., Phila.).

Department of Zoology, The University of Michigan, Ann Arbor, Michigan, *May 19, 1960.*

THE MIDDLE AMERICAN POPULATIONS OF THE CRESTED FLYCATCHER *MYIARCHUS TYRANNULUS*

By WESLEY E. LANYON

The flycatchers of the genus *Myiarchus* are a difficult taxonomic group within a family noted for its difficult genera, such as *Contopus, Elaenia,* and *Empidonax.* There are some 14 to 18 species of *Myiarchus* in the whole of temperate and tropical America, including the West Indies and the Galapagos archipelago. A remarkable uniformity of coloration, a lack of appreciable sexual dimorphism, and interspecific overlap in most mensural characters have led to considerable discrepancy in their systematic treatment. The diagnostic characters that have been used in the past to indicate relationships have often been inadequate and unreliable. The author has undertaken a revision of the genus, based in large measure on field studies of systematically critical breeding populations. This initial paper reports the findings relating to one geographically discrete group, the Middle American populations of the crested flycatchers of the species *Myiarchus tyrannulus,* with special emphasis on the status of the so-called Ometepe Flycatcher (*Myiarchus brachyurus*) of Central America. Consideration is given to the vocalizations which may serve to supplement morphological characters in discerning taxonomic relationships.

HISTORICAL BACKGROUND

The crested flycatchers of México have had an eventful nomenclatural history which need not concern us here. Suffice it to say that the populations of eastern México are now known as *cooperi* (Deignan, 1949) and that *magister* applies to those of western México (see fig. 7 for ranges of forms considered here). The two forms were formerly considered as races of a distinct Mexican species, *Myiarchus mexicanus* (Nelson, 1904; Ridgway, 1907), until Hellmayr (1927), the Fourth Edition of the A.O.U. Check-list (1931) and Griscom (1932) "lumped" them with the geographically distinct and polytypic *Myiarchus tyrannulus* of South America and the Lesser Antilles. These Mexican populations have since been regarded by most workers as conspecific with the disjunct South American group, although not without question (Eisenmann, 1955:67). This author follows Hellmayr, but reserves critical judgment on the matter pending completion of field studies on the South American populations.

A new species of *Myiarchus* was described by Ridgway (1887) from Central America, within the area of the hiatus between the ranges of *mexicanus* and *tyrannulus.* He called this form *brachyurus* and, on the basis of its larger size and shorter tail, he considered it specifically distinct from *Myiarchus nuttingi* which he had described from the same region five years earlier. Allen (1892) contested this specific distinction, commenting that the supposed differences were more likely due to individual variation. This may have influenced Ridgway, who later (1907) reduced *brachyurus* to racial status under *nuttingi.* Nelson, in his monograph (1904), retained the species status of *brachyurus.* The specific distinction between *brachyurus* and *nuttingi* was clearly and adequately summarized by Bangs (1909) and this treatment has been followed by all subsequent workers.

Dickey and van Rossem (1938) were impressed with the apparent intermediacy of their El Salvador specimens between *brachyurus* of Nicaragua and Costa Rica and *tyrannulus* from México, stating that "there would now seem to be little doubt that it is simply a geographical form of *tyrannulus.*" This treatment was accepted by Wetmore (1944) and later followed in the Fifth Edition of the A.O.U. Check-list (1957). In his, manuscript for a forthcoming volume of Peters' Check-list, Zimmer likewise considered

brachyurus to be a Central American race of *tyrannulus*. Other workers have expressed uncertainty about its taxonomic status (Blake, 1953; Paynter, 1955). Rand and Traylor (1954) and the Mexican Check-list (Pac. Coast Avif., 1957) accorded it full species rank.

The most recent addition to the group of forms considered here was an insular population, *M. t. insularum*, described by Bond (1936) and known only from the Bay Islands of Honduras.

MATERIALS AND METHODS

Populations in northern Sonora and southern Arizona were studied during the summers of 1956 and 1957, with aid from the American Philosophical Society (Grant No. 2152) and the Frank M. Chapman Memorial Fund. An expedition from April through June, 1959, co-sponsored by the National Science Foundation (Grant No. G-7083) and the American Museum of Natural History, provided first-hand knowledge of critical populations in Costa Rica, Nicaragua, El Salvador, Guatemala, and southern México, including Yucatán. I am much indebted to Colonel and Mrs. D. S. McChesney of Syracuse, New York, for contributing immeasurably to the success of this expedition.

Emphasis in these field studies was placed on collecting specimens of known sex, vocalizations, habitat preference, and mate preference. Tape recordings were made of representative vocalizations of each of the breeding populations visited, using a Magnemite recorder at 15 inches per second, a preamplifier, and an Altec 660B microphone mounted in a 24-inch parabolic reflector. These recordings involved 54 individuals of the forms being reported on here, ranging in locations from Costa Rica north to Arizona. All recordings were analyzed by ear in the laboratory, and subsequently over 300 representative vocal patterns were selected for analysis with a sound spectrograph. The spectrograms presented here were chosen to demonstrate the extent of geographical variation evident from this analysis.

Over 500 specimens of these forms have been examined. I am indebted to the following for the loan of specimens in their care: James Bond, Pierce Brodkorb, Herbert Friedmann, Thomas R. Howell, Philip S. Humphrey, Richard F. Johnston, George H. Lowery, Jr., Robert T. Orr, Kenneth C. Parkes, Raymond A. Paynter, Frank A. Pitelka, George M. Sutton, Harrison B. Tordoff, Melvin A. Traylor, Dwain W. Warner, and David A. West. Linear measurements, in millimeters, were taken as follows: wing, flattened; tail, from the insertion of the central rectrices; bill length, from the anterior margin of the nostril; width of fuscous stripe along medial side of shaft of outer rectrix, at the midpoint of the shaft. In diagramming statistical analyses, 1.3 times the standard deviation has been plotted on each side of the mean (forming a solid rectangle). Thus, when comparing two samples, non-overlap of the solid rectangles indicates that at least 90 per cent of the individuals of one sample are separable from 90 per cent of the individuals of the other sample with respect to the character being analyzed. Color nomenclature is that of Ridgway (1912). Color of mouth linings was noted in all fresh specimens and photographed in representative individuals.

ANALYSIS OF VARIABILITY

Morphological variation.—Complete descriptions of the plumage of all forms but *insularum* have been published by Nelson (1904) and Ridgway (1907). Special attention is called to Nelson's comments on the problems associated with the marked seasonal changes in plumage within this genus. Coloration of body plumage was found to be remarkably uniform among all but one of these forms and consequently of no value in discriminating between populations. The one exception to this uniformity is the insular population on the Bay Islands of Honduras. The three specimens collected by Bond

(1936) are all somewhat darker above than any mainland population of this group, particularly on the pileum. All fresh specimens examined (none of *insularum*) had mouth linings that were a pale to light ochraceous-buff.

The species of *Myiarchus* differ to some extent with regard to the amount of cinnamon-rufous in the rectrices. Ignorance of the degree of individual variation in this diagnostic character has led to some taxonomic confusion in the genus. Within the crested flycatchers of Middle America, rectrix pattern is the most geographically vari-

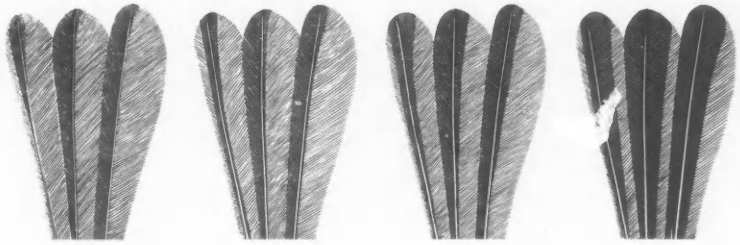

Fig. 1. Extremes in the width of the fuscous stripe of the three outer rectrices in samples of *Myiarchus tyrannulus brachyurus* (A and B), and in *M. t. magister, M. t. cooperi,* and *M. t. insularum* (C and D).

able aspect of plumage coloration. The breeding birds of Nicaragua and Costa Rica (*brachyurus*) have a consistently greater amount of rufous in the tail than do the other Middle American populations. The dark, fuscous stripe, when present, was never greater than 2 mm. wide (average, 1 mm.) in a sample of 78 specimens. Elsewhere, the fuscous stripe in a sample of 282 specimens from the remaining populations varied from 1.5 mm. to 6 mm. (average, 3.5 mm.) with no geographical trend apparent (see fig. 1). The

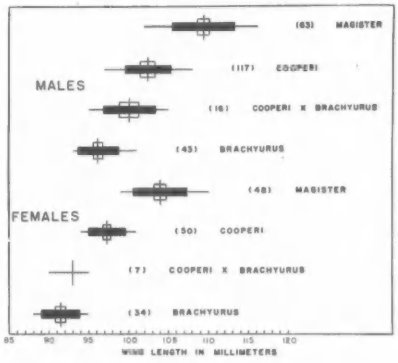

Fig. 2. Statistical analysis of wing length.
Numbers in parenthesis indicate sample size. Horizontal lines represent range; means are indicated by vertical lines; open rectangles indicate twice the standard error of the mean; solid rectangles indicate 1.2 times the standard deviation.

breeding birds of the Pacific lowlands of El Salvador and Honduras have a rectrix pattern that is intermediate between the samples just mentioned. In a sample of 23 specimens, the width of the fuscous stripe varied from 1 to 4 mm. (average, 2 mm.) wide.

Wing length was the least variable, within populations, of the measurements taken (coefficient of variation from 1.82 to 2.73). The three mainland forms, *magister*, *cooperi*, and *brachyurus*, are well differentiated, and equally so, by wing length (fig. 2). The sample of *insularum*, although inadequate to include in the analyses of measurements, suggested no differentiation in size from *cooperi*. The breeding birds of El Salvador and southern Honduras have wing lengths that are intermediate between those of *cooperi* and *brachyurus*. No clinal variation was evident within the ranges of these forms.

Tail length was a somewhat more variable character than wing length (coefficient of variation from 2.34 to 3.64). The two Mexican forms, *magister* and *cooperi*, were less

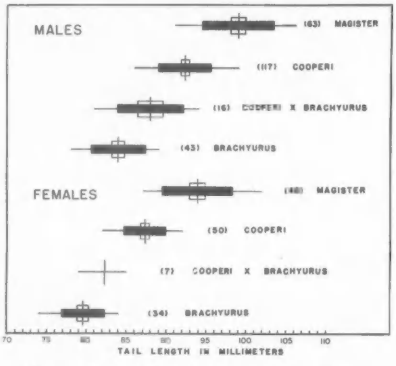

Fig. 3. Statistical analysis of tail length.

differentiated with respect to tail length than to wing length (fig. 3). Although Ridgway, in naming *brachyurus*, meant to denote a shorter tail relative to that of the Nicaraguan *nuttingi*, his name is even more appropriate when *brachyurus* is compared with *cooperi*. The population from Nicaragua and Costa Rica is significantly shorter tailed than the form to the north. As was the case with rectrix pattern and wing length, tail lengths of the birds of El Salvador and southern Honduras were intermediate between those of *cooperi* and *brachyurus*. Once again there was no clinal variation evident within populations.

The populations of western México (*magister*) are significantly longer billed than the remaining forms; *cooperi* and *brachyurus* are not well differentiated by this character (fig. 4). Bill length was a highly variable character within populations (coefficient of variation of 2.51 to 5.31).

There is little sexual dimorphism in these forms. No consistent differences were noted between the sexes with regard to plumage coloration, including rectrix pattern. Males average larger in size throughout Middle American populations, but considerable overlap exists in all measurements. The most reliable dimorphism occurs in the length of the wing, with males averaging 5 mm. longer in all samples studied.

Variation in vocalizations.—In preliminary field studies made in Arizona in 1956–57, the author determined that the vocal repertoire of *magister* consisted of four basic patterns. Various combinations of these basic patterns were sometimes rendered, there-

by extending the apparent variety of the repertoire. The most distinctive of these patterns, that is, the one found to be most useful in distinguishing *magister* from the two sympatric species of *Myiarchus* in Arizona, is illustrated in the top row of spectrograms in figure 5. It is rendered with great intensity, may be heard at a considerable distance, and is not to be found in the repertoire of any other *Myiarchus* of North or Middle America. Spectrograms of the most distinctive vocal patterns of these other *Myiarchus* flycatchers are shown in figure 6 for comparative purposes.

Analysis of tape recordings made in 1959, from representative populations elsewhere in Middle America, reveals that this same basic repertoire is shared by all of the forms being considered here (see fig. 5). Geographical variation in these basic patterns was found to be no greater than the individual variation recorded within populations. The only consistent geographical variation, a slight rise in frequency from north to

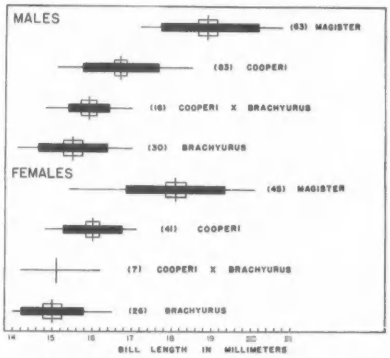

Fig. 4. Statistical analysis of bill length.

south, is probably correlated with body size. In the top row of spectrograms in figure 5, for example, the patterns of *brachyurus* at the left are at a somewhat higher frequency than those at the right, which are of the larger *cooperi* and *magister*.

By collecting specimens whose vocalizations were previously recorded on tape it was possible to demonstrate that both sexes of these Middle American forms render all of these basic vocal patterns, although the males tend to be more vociferous. Vocal patterns *per se* cannot be used, therefore, as a means of sexing birds in the field.

In view of the great morphological similarity among the species of *Myiarchus*, the homogeneity of the vocal repertoire and its distinctiveness from that of sibling species suggests that vocal characters may be important in species discrimination among these birds. Preliminary investigation supports this contention, but carefully controlled experiments are needed. A field experience in eastern Guatemala is a case in point. A search for *cooperi* breeding in this remote area led the author to clearings in the rain forest near Sebol, just south of the Peten border. A pair of *cooperi* was heard from beyond an impenetrable tangle of low vegetation. An initial playback of a recording of *M. tuberculifer*, a sympatric species, brought no response from the distant birds. But a second recording, made of *brachyurus* in Costa Rica, brought an immediate response. The pair of *cooperi* appeared and darted nervously about in the vicinity of the speaker. They were quite vociferous and were subsequently recorded and collected.

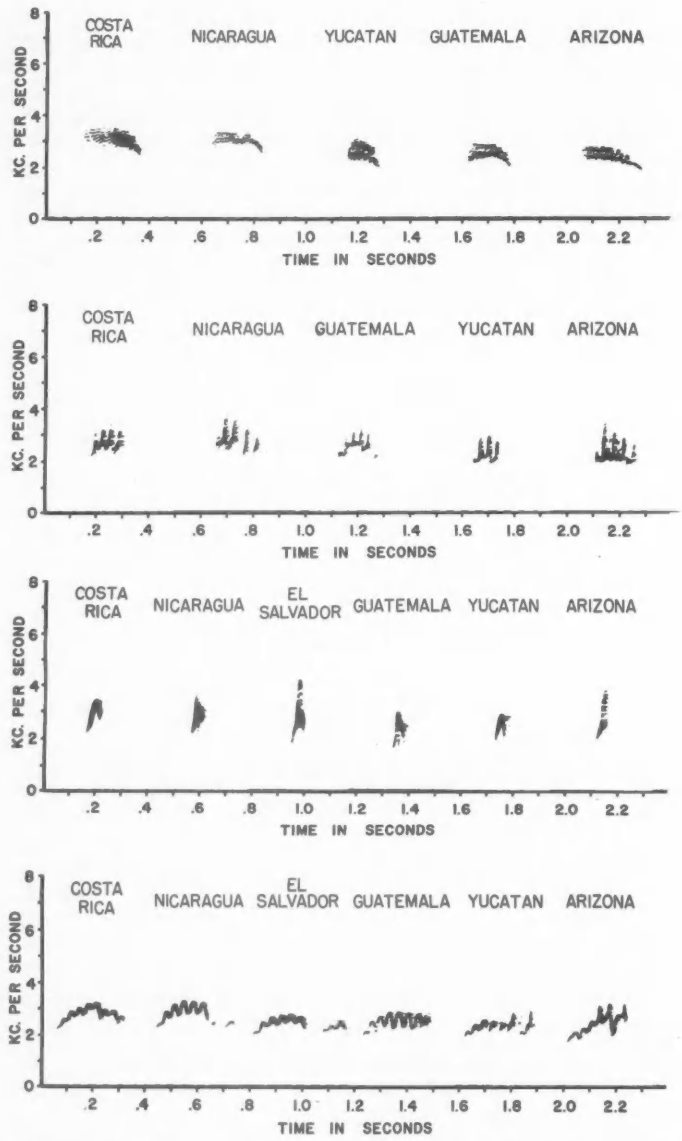

Fig. 5. Sound spectrograms of four vocal patterns characteristic of *Myiarchus tyrannulus* in Middle America.

GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTION

The breeding ranges of the forms under consideration here are presented in figure 7. The distribution of *Myiarchus tyrannulus magister* is roughly coincident with the Lower Sonoran Zone of Arizona and Sonora and the Arid Tropical Zone of the Pacific lowlands of México. Although occurring casually throughout the desert-mesquite associations, tropical deciduous woodlands, and thorn forests, *magister* is most abundant among the giant cacti and riparian communities where it can find natural cavities or abandoned

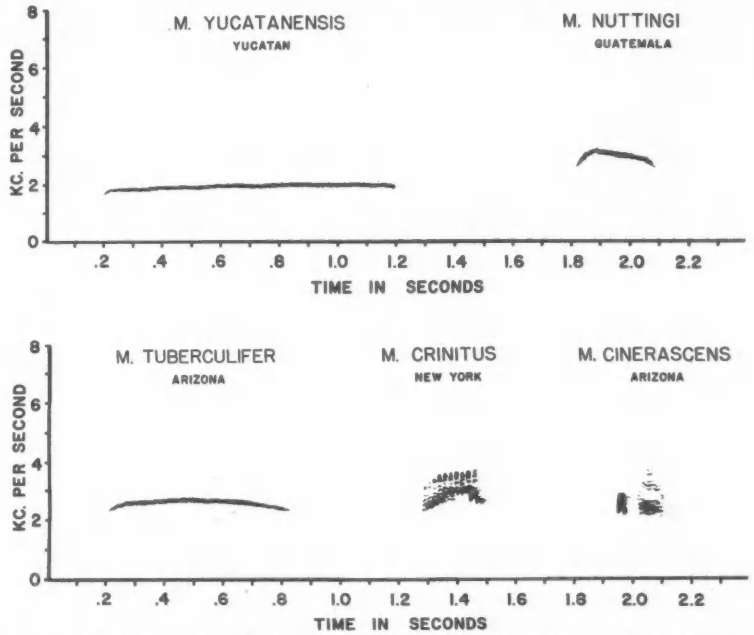

Fig. 6. Sound spectrograms of vocal patterns characteristic of five other species of *Myiarchus* occurring in Middle and North America.

woodpecker holes of substantial size for its nest sites. It has successfully colonized the Tres Marías Islands but without differentiation from the mainland population. The southernmost breeding specimens examined by the author that can unquestionably be assigned to this race were two males taken in the isthmus region of Oaxaca (U.S. Nat. Mus.). Breeding *tyrannulus* in the Pacific lowlands of the isthmus region are apparently of extremely local occurrence and gene exchange with *cooperi* is therefore restricted. In the northern part of its range, at least, *magister* is migratory. Two nonbreeding specimens from coastal Chiapas (U.S. Nat. Mus.; Brodkorb Coll.), obviously assignable to this race, suggest a limited winter movement south of the breeding range.

In the lowlands bordering the Gulf of México and the Caribbean, *M. t. cooperi* occupies a greater variety of habitats than the western Mexican race, ranging from mesquite and thorn forest in the north (most abundant in riparian communities) to clearings in tropical evergreen and rain forest in the south. The requirement for larger trees as nest sites is probably not as stringent in this smaller race, but its nesting habits are

otherwise identical. Although essentially a race of the Gulf lowlands, three breeding specimens from the isthmus region of Oaxaca (U.S. Nat. Mus.; Am. Mus. Nat. Hist.) are closer to *cooperi*. Intergradation with *magister* no doubt occurs in a limited area of eastern Oaxaca. The specimens taken by Edwards and Lea (1955) near Monserrate, Chiapas, are typical *cooperi* and constitute the only definite breeding record known to the author for the Pacific lowlands of Chiapas. However, a worn male taken in late April by Brodkorb (Univ. Mich. Mus. Zool. 102,605) near Pijijiapan, Chiapas, is also

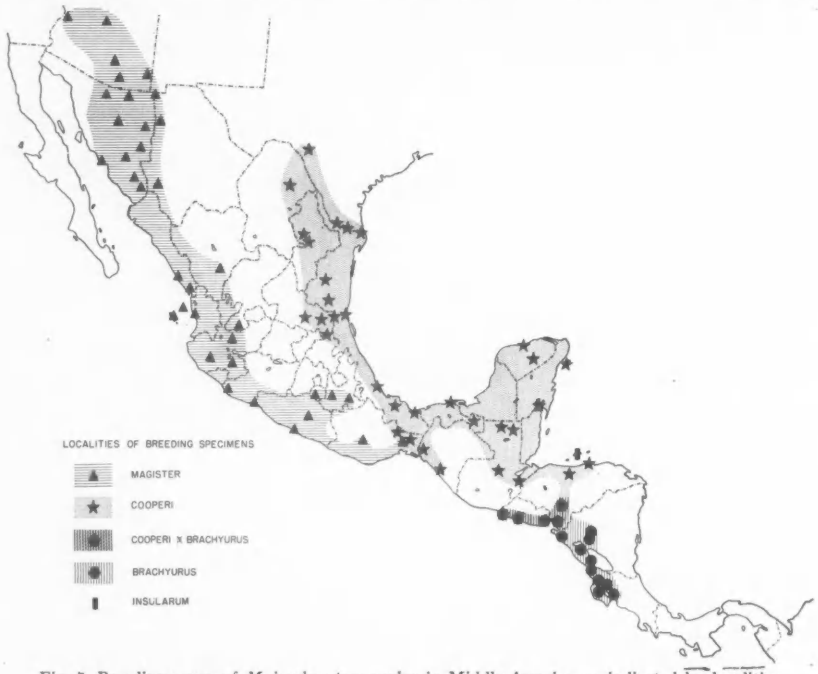

Fig. 7. Breeding range of *Myiarchus tyrannulus* in Middle America, as indicated by localities of specimens examined.

typical *cooperi* and suggests that the race may breed locally at least that far south in the Pacific drainage. Its absence as a breeding bird in the Pacific lowlands of Guatemala was reported by Griscom (1932) and substantiated by the author in 1959, thus creating an interesting hiatus in the breeding range of the species along the Pacific drainage (see fig. 7). The race has successfully colonized Cozumel Island off Quintano Roo but without differentiating from the mainland population.

The southeasternmost breeding records of *cooperi* known to the author for the Caribbean lowlands are from northern Honduras: two juveniles (Carnegie Museum) collected by Twomey in June near Coyoles, and a molting female (U.S. Nat. Mus.) taken at Trujillo in September. The race is migratory in the northern part of its range. In winter, it is rather widely distributed throughout Guatemala, including the Pacific drainage. The southernmost wintering specimens are from El Salvador (Dickey Coll.; Mus. Vert. Zool.; Chicago Nat. Hist. Mus.).

The author has no knowledge of the voice, habits, or ecology of *M. t. insularum* on the Bay Islands of Honduras. It is clearly allied to *cooperi*, from which it differs only in a darkening of the upper parts. That even this degree of differentiation should have occurred is of interest in view of the lack of differentiation in insular populations of *magister* on the Tres Marías and of *cooperi* on Cozumel.

The breeding birds of southern Honduras and of the Pacific coast of El Salvador and Honduras are morphologically intermediate between *cooperi* and *brachyurus* (see figs. 2 to 4). Gene exchange between this intermediate population and typical *cooperi* is probably accomplished via the Honduras depression (Carr, 1950) which connects the Caribbean and Pacific lowlands, and this population is contiguous on the south with typical *brachyurus*. The westernmost specimens in this intermediate population were collected by van Rossem (Dickey Collection; Chicago Nat. Hist. Mus.) in extreme western El Salvador. The absence of *tyrannulus* in the Pacific lowlands of Guatemala has already been discussed. The controversial specimen of "*brachyurus*" from Tonalá, Chiapas (U.S. Nat. Mus. 147638) is a female *cooperi*.

Aside from its morphological intermediacy, this rather small breeding population is of interest because of its apparent ecological restriction, in the coastal plain, to mangrove communities (Dickey and van Rossem, 1938; Rand and Traylor, 1954, and confirmed by the author in 1959). It is curious that there should be so much seemingly suitable habitat for *M. tyrannulus* unoccupied in this region—habitat of a type in which *brachyurus* breeds commonly only a short distance to the south in Nicaragua. There is no evidence of a comparable ecological restriction in any other Middle American population of *tyrannulus*. There is apparently some movement of these birds inland during the fall and winter (Dickey and van Rossem, 1938).

The geographically limited but well-defined race *M. t. brachyurus* is the resident population of the tropical, deciduous woodland of western Nicaragua and northwestern Costa Rica. No specimens are known from south of the Gulf of Nicoya, where the vegetation changes rather abruptly under the influence of a much greater rainfall. The nesting and foraging habits of this smallest Middle American race appear to be identical with those of the larger Mexican forms.

SUMMARY AND CONCLUSIONS

This paper is a report on one geographically discrete group of the flycatchers of the genus *Myiarchus*, the Middle American populations of *Myiarchus tyrannulus*. Special emphasis is placed on the status of *brachyurus*, the Ometepe Flycatcher of Central America, which is shown to be a race of *Myiarchus tyrannulus*. Spectrographic analysis of vocalizations is used to supplement morphological characters.

Plumage coloration was found to be remarkably uniform among all populations considered, with geographical variation evident only with respect to rectrix patterns and a darkening of the upper parts of an insular race. The breeding birds of Nicaragua and Costa Rica, the form *brachyurus*, differ from all other populations in having significantly larger amounts of cinnamon-rufous in the tail.

The three mainland forms (*magister*, *cooperi*, and *brachyurus*) are well differentiated with regard to wing and tail length, but less so with regard to bill length. The breeding birds of the Pacific lowlands of El Salvador and Honduras are intermediate between *cooperi* and *brachyurus* in rectrix pattern and size. Sexual dimorphism is limited in all populations and consists of slightly larger average size in males.

All populations considered, including *brachyurus*, share the same basic repertoire of vocalizations, which differs substantially from that of the other flycatchers of the

genus *Myiarchus* of North and Middle America. Preliminary investigation suggests that vocal characters may be important in species discrimination among these birds.

Four races of *Myiarchus tyrannulus* are recognized for Middle America, and a discussion of the geographical and ecological limits of their distribution is included. The hiatus in the breeding range on the Pacific drainage of Chiapas and Guatemala and the ecological restriction of the breeding birds of El Salvador and southern Honduras to mangrove communities are unexplained aspects of the distribution of the species.

LITERATURE CITED

Allen, J. A.
1892. On a collection of birds from Chapada, Matto Grosso, Brazil, made by Mr. H. H. Smith. Part II.—Tyrannidae. Bull. Amer. Mus. Nat. Hist., 4:331–350.

American Ornithologists' Union
1931. Check-list of North American birds. Fourth Ed. (Published by the Union, Lancaster, Pa.).
1957. Check-list of North American birds. Fifth Ed. (Published by the Union, Baltimore, Md.).

Bangs, O.
1909. Notes on some rare or not well-known Costa Rican birds. Proc. Biol. Soc. Wash., 22:29–38.

Blake, E. R.
1953. Birds of Mexico (Univ. Chicago Press).

Bond, J.
1936. Resident birds of the Bay Islands of Spanish Honduras. Proc. Acad. Nat. Sci. Phila., 88:353–364.

Carr, A. F., Jr.
1950. Outline for a classification of animal habitats in Honduras. Bull. Amer. Mus. Nat. Hist., 94:563–594.

Deignan, H. G.
1949. The correct name for the Mexican crested flycatcher. Condor, 51:270.

Dickey, D. R., and van Rossem, A. J.
1938. The birds of El Salvador. Field Mus. Nat. Hist., Zool. Ser., 23:1–609.

Edwards, E. P., and Lea, R. B.
1955. Birds of the Monserrate Area, Chiapas, Mexico. Condor, 57:31–54.

Eisenmann, E.
1955. The species of Middle American birds. Trans. Linn. Soc., N. Y., 7:1–128.

Griscom, L.
1932. The distribution of bird-life in Guatemala. Bull. Amer. Mus. Nat. Hist., 64:ix+1–439.

Hellmayr, C. E.
1927. Catalogue of birds of the Americas. Field Mus. Nat. Hist., Zool. Ser., 13, pt. 5.

Nelson, E. W.
1904. A revision of the North American mainland species of *Myiarchus*. Proc. Biol. Soc. Wash., 17:21–50.

Pacific Coast Avifauna
1957. Distributional check-list of the birds of Mexico. Part II. Pac. Coast Avif., 33:1–435.

Paynter, R. A., Jr.
1955. The ornithogeography of the Yucatan Peninsula. Peabody Mus. Nat. Hist., Yale Univ., Bull. 9:1–347.

Rand, A. L., and Traylor, M. A.
1954. Manual de las aves de El Salvador (Univ. El Salvador).

Ridgway, R.
1887. A manual of North American birds (J. B. Lippincott Co., Phila.).
1907. The birds of North and Middle America. Pt. IV. Bull. U.S. Nat. Mus. 50.
1912. Color standards and nomenclature (Published by the author, Washington, D.C.).

Wetmore, A.
1944. A collection of birds from northern Guanacaste, Costa Rica. Proc. U.S. Nat. Mus., 95:25–80.

American Museum of Natural History, New York, New York, March 23, 1960.

LIFE HISTORY OF THE CACTUS WREN

Part III: THE NESTING CYCLE

By ANDERS H. ANDERSON and ANNE ANDERSON

This paper is a continuation of our report on the life history of the Cactus Wren (*Campylorhynchus brunneicapillus*) in the vicinity of Tucson, Arizona. In Part I (1957) we described the winter activities, roosting nests, song, territorial establishment, and pair formation. Part II (1959) followed with a discussion of the breeding nest, the defense of the territory, and the time of laying of the first egg. We have banded 18 additional Cactus Wrens in the Kleindale Road area since May 21, 1957, when Part I was completed. The total is now 89.

THE EGGS

The eggs in a Cactus Wren's nest cannot be seen from the outside, even with a mirror, for they are sometimes virtually hidden among the feathers on the floor of the nest cavity. We made no systematic attempts to remove them for inspection, weighing or marking, for the possibility of breakage during handling in the confined nest space was too great. Our limited population of Cactus Wrens offered little opportunity for comparative studies of size, color, or shape of eggs. The eggs were counted by inserting a hand into the vestibule and enlarging it by expanding the fist and fingers as the hand moved inward and downward. The spiny, easily detached joints of the jumping cholla (*Opuntia fulgida*) proved to be especially vicious and treacherous. Pliers with which to remove the spines from hands, wrists, and forearms were always carried along. Finally an aluminum sleeve was constructed which afforded considerable protection. It was thrust into the nest entrance, but it was still necessary to use the fingers to enlarge the diameter. Frequently some of the joints of the cholla had to be bent aside or removed to facilitate inspection. What was an easy, accessible route for the occupants was often a dangerous and difficult one for larger intruders. The damage to the nest and its surroundings during inspection was sometimes rather extensive. Nevertheless, no desertions occurred, even when the visit took place just before the first egg was laid or immediately after.

The female began roosting at night in her newly constructed breeding nest as soon as it was well covered over and some of the lining was in place. Sometimes she occupied it a week before the first egg was laid. Meanwhile, the installation of additional lining continued, but at a reduced pace, by both adults. In those cases where the female appropriated the male's roosting nest for her breeding nest, the refurbishing of the interior began anew. In February of 1959 it was not entirely clear whether the nest she took over was at first intended to be a roosting nest. It had been chosen because of the many disturbances the female suffered in her winter quarters in the pyracantha bush near our front porch with its electric light. She occupied the male's roosting nest for 11 nights before she laid the first egg of the year.

Eggs were laid at the rate of one a day on consecutive days in early morning after sunrise. Possible exceptions to this routine occurred in 1941. Two eggs in nest 35B were found on February 25 at 5:45 p.m. The third egg was laid on the 26th after 7:20 a.m. On the following day the nest was visited at 7:15 a.m. and 5:45 p.m., but only three eggs were counted. The female was frightened out at the first visit, and may have had to lay the egg before returning to the nest. The fourth egg was found on February 28. The fourth clutch of 1941 contained two eggs on the evening of June 12. On the 13th at 7:00 p.m. a broken egg was found on the ground beneath the nest, and there was only one egg in the nest. No further laying occurred at least up to 6:50 p.m. on the 14th. When we next visited this nest at 7:00 p.m. on the 15th, another egg had been laid.

Unfortunately we did not find the first egg of 1959 until late afternoon. The second egg was laid on February 20 between 7:30 a.m. and 8:30 a.m.; the third was laid on the 21st between 7:48 a.m. and 8:50 a.m. In March of 1947 the fourth and last egg of the clutch was laid between 7:23 a.m. and 8:01 a.m., the others in order, before 7:25 a.m., 7:30 a.m., and 7:20 a.m. We doubt that a female remains very long in the nest after she has laid. In 1947 the time required to lay the fourth egg after the female entered her nest was 38 minutes; in 1959 it was 62 minutes for the third egg. These would be extremely long incubation intervals, especially since they occurred early in the morning when the wren needed food. Therefore the layings in 1947 and 1959 probably took place just before the female was seen to leave the nest. In March of 1944, 2 eggs of one clutch

Table 1

Number of Eggs Per Clutch

Year	1st	2nd	3rd	4th	5th	6th
1939	3 (est.)	3	3 (est.) (F)*	4		
1940	4	4				
1941	4 (F)	5	5	3 (F)	4 (F)	
1942	4	3 (est.)				
1942	4	5				
1943	3					
1944	3 (F)	1 (F)	4	3 (est.)		
1944	3 (F)					
1945	3	4	4 (F)			
1945	4 (F)	4				
1945	3					
1947	4	3 (est.)				
1947	4	3 (est.) (F)				
1948	3 (est.)					
1952	3 (est.)					
1953	3	3	3			
1954	4 (F)	3 (F)				
1955	3 (est.)	3 (est.)	3 (est.)			
1956	4	4	4 (F)	4 (F)		
1957	3 (F)	4	4			
1958	3	4	5	5 (F)	4 (F)	4 (F)
1959	3	3	3 (F)			

* F indicates failure of clutch.

were laid before 7:20 a.m. on consecutive days; the next egg was laid after 7:20 a.m. A similar situation, just noted, was observed in 1947 when the fourth egg was laid somewhat later in the morning than the first three. The first eggs of two clutches in June and July, when day length is greater, were laid earlier than those in February and March, but the last eggs of these clutches were held until after 8:00 a.m. and 7:10 a.m., respectively. Apparently, as laying progresses, the time required for egg formation increases to more than 24 hours.

Available data on the number of eggs in each annual series of clutches, which we found in nests in the Kleindale Road area, are shown in table 1. When nests were inaccessible, as happened occasionally in neighbors' lots, we were compelled to estimate the number of eggs later, from the number of fledglings we saw being fed by the parents. Thus these estimates are minima, for the actual number of eggs may have been larger. Complete failures of nesting attempts are marked (F). They are so designated when no young were fledged from a nest. A question mark indicates that the outcome of the nesting attempt is uncertain. Only one wren was fledged from the first brood in 1939; we had failed to discover this nest in time to determine the size of the clutch.

An assumption that a minimum of 3 eggs was laid seems safe. We have never found less than 3 eggs in a complete set. In 13 of the 22 years the first clutches contained 3 eggs each; in the other 9 years there were 4 eggs in each first clutch. The average is 3.41 eggs per clutch. Bent (1948:225) reported that the usual set "consists of four or five eggs, most commonly four; but as few as three may constitute a full set, and as many as six or even seven have been found in a nest," but no tabulation of dates, or which brood was involved, is given. Brandt (1951:187) says "the usual clutch numbers three or four, with an infrequent five." It is interesting to compare these statements with a total of 24 sets of eggs collected in the months of February and March by George F. Breninger (field note book) near Phoenix, Arizona, in 1896, 1897, 1898, 1899, and 1901. There were 10 clutches with 3 eggs each, 12 with 4 eggs each, and 2 with 5 eggs each. The average was 3.67 eggs per clutch.

Table 2

Hatching and Fledging Success

Year	Nest	Eggs laid	Hatched	Per cent hatched	Fledged	Per cent fledged
FIRST CLUTCH						
1939	28B	3 (est.)			1	
1940	6M	4	4	100	4	100
1941	35B	4	Destroyed by boys			0
1942	7E	4	4	100	4	100
1942	43B	4	4	100	4	100
1943	100	3	3	100	?	
1944	6AB	3	Eggs disappeared			0
1944	66A	3	Eggs disappeared			0
1945	14C	3	1	33.3	1	33.3
1945	37D	4	Nest destroyed			0
1945	51C	3	1	33.3	?	
1947	19C	4	3	75	3	75
1947	6AJ	4	3	75	3	75
1948	6AK	3 (est.)			3	
1952	78A	3 (est.)			1 (est.)	
1953	25C	3	3	100	3	100
1954	25D	4	4	100	0	0
1955	6AQ	3 (est.)			3	
1956	67E	4	?		2	50
1957	93B	3	Eggs disappeared			0
1958	5K	3	3	100	3	100
1959	17L	3	3	100	3	100
SECOND CLUTCH						
1939	6G	3	3	100	3	100
1940	32A	4	4	100	4	100
1941	27B	5	5	100	5	100
1942	6T	3 (est.)			3	
1942	60A	5	4	80	?	
1944	6AC	1	Egg disappeared			0
1945	23F	4	4	100	4	100
1945	46E	4	3		?	
1947	6AK	3 (est.)			2 (est.)	
1947	75A	3 (est.)	2 (est.)		0	0
1953	56B	3			2 (est.)	
1954	6AR	3	1		0	0
1955	27E	3 (est.)			3	
1956	27H	4			2 (est.)	
1957	96C	4	4		3 (est.)	
1958	25G	4	4	100	4	100
1959	P5	3	3	100	3	100

Table 2, Continued

Year	Nest	Eggs laid	Hatched	Per cent hatched	Fledged	Per cent fledged
THIRD CLUTCH						
1939	6H	3 (est.)			0	
1941	35C	5	3	60	3	60
1944	23E	4	4	100	3	75
1945	6AF	4	1 (est.)		0	0
1953	6AP	3	2 (est.)		2 (est.)	
1955	6AT	3 (est.)	1 (est.)		1 (est.)	
1956	17D	4	0		0	0
1957	27I	4			3	75
1958	5L	5	5	100	5	100
1959	P5	3	0			0
FOURTH CLUTCH						
1939	7D	4	4	100	3	75
1941	34A	3 (est.)	0			0
1944	6AC	3 (est.)			3 (est.)	
1956	6AV	4	1 (est.)		0	0
1958	25H	5	3	60	0	0
FIFTH CLUTCH						
1941	32B	4	1 Destroyed by cat			0
1958	17J	4	0			0
SIXTH CLUTCH						
1958	92D	4	0			0

Brandt (1951:190) has suggested that in a period of prolonged drought, such as preceded the laying in 1949, the low number of 3 eggs, which he found in a nest near Rillito Creek, may have been due to the wren anticipating a reduced food supply for its offspring. There is little in our data to support this view. The precipitation from October 1, 1939, to the laying of the first egg on February 20, 1940, was 2.08 inches. The following winter almost four times as much rain was recorded in a similar period. Yet the clutches for each of these years contained 4 eggs each, the first eggs being laid on February 20 and 24, respectively. In the spring of 1953, after 4.84 inches of rain, a set of 3 eggs was laid. Then a month earlier in 1954, and after but 1.21 inches of rain, a clutch of 4 eggs was laid.

Six of the 22 first clutches in table 1 failed completely. The set of 4 eggs in 1941 was destroyed; the female wren was missed the same day. HM-23 found a new mate, HF-29, who laid 5 eggs in their new nest. In 1944, he had another female, HF-39. The first clutch of 3 eggs failed to hatch. They tried again in a new nest, but the first egg or two were destroyed almost at once. Their third attempt in another nest, this time with 4 eggs, succeeded. In 1954 the first clutch of 4 eggs was abandoned when the noband female died in the nest. The noband male obtained another female, who laid only 3 eggs in the next clutch. This was probably her first set of the year. The first try in 1957 by HM-70 and HF-71 failed when the 3 eggs and the male were lost. When she found another mate, she laid 4 eggs in her new nest. Although there is a hint here of a tendency to lay a larger clutch after the failure of a first attempt, in only one of the above instances was the same pair involved. A female was replaced in the first and second examples and a male in the fourth. An increase in clutch size, after a failure, would appear advantageous to the species, provided the added burden of feeding could be carried successfully. Table 1 shows that in three of the years, 1942, 1945, and 1958, clutch size increased after a successful first brood, and, with the exception of one of the clutches in 1942, it remained as large as in the first brood in the other years. The estimate of 3 eggs in 1942 could be low.

Hatching and fledging success and percentages of clutches that failed completely are

given in tables 2 and 3. The failure of a nest in 1944 after one egg was laid has been excluded and the four nests at which fledging could not be determined have been excluded from the summary of per cent fledged in table 3. In this table the rapid decline in the number of clutches attempted after the first, and the increase in failures after the second are very striking. Although as many as six clutches were laid in a season, the maximum number of broods raised was three. If we regard a nesting attempt as successful if at least one wren is fledged, we can summarize as follows: in one of the years no young were fledged; in four of the years one brood was raised; in nine of the years two broods were raised; and in four of the years three broods were raised.

Table 3

Summary of Clutch Failures

Clutch	Number of clutches	Average eggs per clutch	Clutches that failed	Per cent of failure
1st	22	3.41	6	27.3
2nd	16	3.63	3	18.7
3rd	10	3.80	4	40
4th	5	3.80	3	60
5th	2	4.00	2	100
6th	1	4.00	1	100

None of the female nestlings, or the few immature wrens from adjacent territories which we banded, remained to breed the following year. Since the age of the adult females at the time of banding was not known, we have no evidence to indicate that any of them laid a larger clutch in their second or third year with us than they did in their first. Our meager data show that HF-39 laid 3 eggs in her first clutch of 1944 and 3 in 1945; HF-71 laid 3 eggs in 1957, and 3 in 1958.

INCUBATION

Incubation was performed entirely by the female. So far as we could observe, the male never entered and remained in the breeding nest when the female left to search for food. The nest was occupied by the female the night after the first egg was laid, and the female continued to occupy the nest nightly without interruption thereafter. Daytime incubation was extremely irregular on the first day. In fact, it is doubtful if effective warming occurred at all. In nests that we inspected on the first day in midmorning, at noon, and in the afternoon, we found the egg decidedly cold to the touch and the female was absent. Cold eggs were also found in some nests in the early forenoon of the second and third day. Does embryonic development begin as soon as the first egg is laid, or does it await the initiation of regular, attentive incubation after the final egg? The Cactus Wren could sleep in the adequately long vestibule of her nest, awaiting completion of egg laying, without transferring any of her body heat to the egg, but we do not believe she does this. We seldom inspected breeding nests at night, for a frightened wren would have great difficulty in finding its way back. However, a wren that was accidentally disturbed at 8:55 p.m. on April 27, 1941, left a very warm, single egg in the nest. Evidently she had been sitting on the egg. Swanberg (1950) has shown that some species of birds can actually sit in the nest without warming the eggs appreciably. In a careful study of the European Blackbird (*Turdus merula*), Enemar (1958) found that incubation began before the clutch was complete. When the Cactus Wren enters her breeding nest she retreats to the far end into the depressed cavity, just as she does in her roosting nest. It would seem illogical to assume that a bird which for the greater part of the year regularly roosts in a deep cavity would, when the first one or

two eggs are laid, forsake this comfortable place to roost in the narrow, tunnel-like vestibule in which it cannot turn around. As further evidence of early incubation and warming we have the observed fact that all of the eggs never hatched on the same day.

Using Heinroth's (1922) rule and its elaboration by Swanberg (1950) for the determination of the incubation period, we checked the time from the laying of the last egg to the hatching of the last young. Most nests were inspected twice a day, in the early morning and in early evening. Some could be visited only in the late afternoon. The period of incubation was 16 days in nine nests in which we have accurate data. In three other nests with incomplete data we estimate it to be also 16 days, but there is a possibility it could have been 15.

Our observations are at variance with those of Hensley (1959:89) who reported that "incubation lasted 17 days in two nests." In one of these, however, he states that "the clutch of three eggs was completed on March 29 and on April 16 the nest contained three newly hatched young." If the last one hatched on April 16, the incubation period was actually 18 days.

We were able to study incubation attentiveness in considerable detail at nest 19C in 1947. Data from two complete days, from the awakening of the female to her retirement are available. In addition, we have another day with only 18 minutes missing. The first egg was found on March 26 when we examined the nest at 7:25 a.m. Both adults were observed carrying lining material to the nest from 9:25 to 10:15 a.m. On the last trip the female, HF-50, remained in the nest at least 5 minutes. On March 27 we watched the nest from 6:50 a.m. to 9:37 a.m. The six periods on the nest varied in minutes as follows: 10, 15, 7, 6, 0.5, 5; the periods off the nest were: 15, 16, 7, 5, 53.5, 27. Average time on the nest was 7.3 minutes; average time off was 20.6 minutes. We checked the nest at 7:30 a.m.; it contained 2 eggs. The female flew out as we approached. Evidently incubation was already in progress, but it was very irregular, with only 26 per cent of the time devoted to warming the eggs. HF-50 carried bits of lining material to her nest at every visit. At long intervals the male brought food to her as she sat inside. We found the third egg on March 28, at 7:20 a.m., but no further observations were made that day.

On March 29 we began our watch before sunrise. Our observation post was a bedroom window facing the nest only 15 feet away. It was more comfortable than a blind; the wrens suffered no disturbance, but the station had the disadvantage of narrowing our field of view, so that the wrens could not be watched after they left the nest. We remained at our post continuously until 5:22 p.m. After a short absence, we began again at 5:40 p.m. and watched until HF-50 retired at 6:48 p.m. The first song of the male came at 5:58 a.m. HF-50 left nest 19C at 6:03 a.m. The sky was clear and there was no wind. The official University of Arizona minimum temperature was 46°F. We inspected the nest at 6:15 a.m., when the female was absent, and counted 3 eggs. Eighty minutes elapsed before HF-50 returned to her nest. Meanwhile her mate had visited it once and entered, but he left and continued singing in the vicinity. How the male finds the eggs is no problem at all; he merely looks inside the nest. The female now remained in the nest for 38 minutes. The fourth and last egg was probably laid at this time. (We did not inspect the nest until 2:50 p.m.; it contained 4 eggs then.) By 5:22 p.m. HF-50 had sat on the eggs 21 times and had been off the nest 22 times. The average time on the eggs was 11.6 minutes; average time off was 19.8 minutes. The length of the periods on the nest varied from one to 42 minutes; off periods varied in length from five to 80 minutes. HF-50 incubated 35.9 per cent of the daylight time. Following our resumption of observations at 5:40 p.m. there was one more period on the nest of nine minutes, beginning at 6:27 p.m., and one off period of 12 minutes, after which the female retired.

The addition of these two periods to the total has only a slight effect on the averages just presented. On the succeeding six days lack of time limited our observations to about an hour each day in the forenoon. The data we obtained are too fragmentary to permit any safe conclusions, except that the lengths of the extreme on and off periods appeared to decrease.

It was possible to observe this nest for a whole day on April 5, the seventh day of incubation of the full clutch. We recorded 28 attentive periods and 29 inattentive

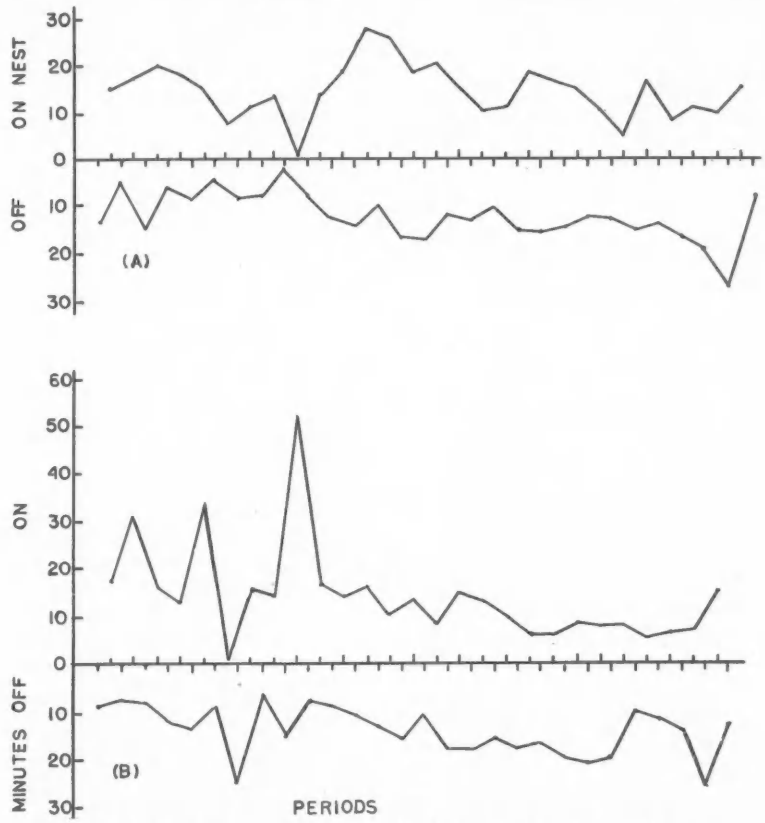

Fig. 1. Incubation attentiveness at nest 19C. A, April 5, 1947; B, April 12, 1947.

periods from 6:17 a.m. to 6:50 p.m. The former averaged 14.8 minutes; the latter averaged 11.7 minutes. The range of variation was one to 28 minutes and two to 26.5 minutes, respectively. For the distribution of these "on" and "off" periods in the course of the day see figure 1A. It is interesting to note the wave shape of the "on" periods. The periods occur in groups, and a group of long periods is followed by a group of short ones, and these are followed by another group of long ones, the peaks and depressions decreasing and smoothing out in the afternoon. This cyclic behavior is present but not

so pronounced in the curve of the "off" periods. There is a distinct lengthening trend in the "off" periods as the day becomes warmer. The temperatures on April 5 were: maximum 70°F., minimum 38°F., and mean 54°F. The length of HF-50's day of activity was 12 hours and 33 minutes; 54.9 per cent of this time was spent in incubation.

On April 12, 1947, the day before the first egg hatched, the female left nest 19C at 5:56 a.m. She retired at 6:52 p.m. In the course of this day of 12 hours and 56 minutes, she devoted 50.3 per cent of her time to the nest. There were 27 attentive periods averaging 14.5 minutes each, and 28 inattentive periods averaging 13.8 minutes. The variation was from one to 54 minutes in the attentive periods, and six to 26 minutes in the inattentive ones. Figure 1B gives the distribution of these periods. Temperatures on this day were: maximum 79°F., minimum 48°F., mean 63.5°F. With the exception of the first part of the day, the curve of "on" periods has smoothed out considerably. The extremely long attentive period of 54 minutes began at 10:00 a.m. It is difficult to explain, but it may have been induced by an immature Curve-billed Thrasher (*Toxostoma curvirostre*) which climbed into the cholla and moved about beneath the wren's nest at this time. We have observed that Cactus Wrens will enter and remain inside their breeding nests when there is a possibility of intrusion by neighboring birds. Far more difficult to account for is the occurrence of the one-minute attentive periods. There was one each on March 29, April 5, and April 12. No disturbances of any nature could be observed at these times. On April 12, the male, HM-54, visited nest 19C eight times between 7:07 a.m. and 1:50 p.m. Half of these visits occurred when the female, HF-50, was in the nest; the male then remained in the vestibule from 0.5 to 1.5 minutes. On those visits when he discovered that the female was absent, he left at once. On his last trip at 1:57 p.m. he carried a small object, apparently an insect, into the nest, but HF-50 was not there. Evidently he swallowed the insect, for he left without it. At 6:41 p.m. the 4 eggs had not yet hatched.

The female continued to bring bits of lining material, such as fine grasses and small feathers, to her nest throughout the entire incubation period. For the first week, the male assisted in this work, but he did so very irregularly. He visited the nest occasionally, without nest material, apparently out of curiosity or in search of his mate. When she was absent, he would enter, but he remained inside only a few seconds before flying away. Courtship feeding was seldom noted. It probably occurred no oftener than three or four times a day at the beginning of incubation, and apparently it ceased altogether before the eggs hatched. We did not observe any feeding on April 12.

HATCHING

The time required for all the eggs to hatch in the completely successful nests varied as follows: in 3 nests with 3 eggs each, the time was 3, 2, and 2 days; in 5 nests with 4 eggs each, the time was 2, 2, 3, 2, and 3 days; in 2 nests with 5 eggs each, the time was 3 and 3 days. In a nest of 3 eggs in which one did not hatch, 2 hatched on the same day; in another nest with 4 eggs, in which one did not hatch, the remaining 3 hatched in 2 days. Six of the females hatched one egg on the first day; 7 hatched 2 eggs the first day, and one hatched 3 eggs the first day. It was not necessarily the largest clutches which produced the most nestlings on the first day of hatching. Only one egg hatched on the first day in nest 5L; 2 more hatched on the following day, and the last 2 on the next day. The small samples available show no important differences in time between the early season broods and those in later months.

FEEDING OF NESTLINGS

On April 13, 1947, one of the eggs in nest 19C was found to be hatched at 7:35 a.m.; by 5:20 p.m. another had hatched. We were unable to make any further observations

until 5:50 p.m. At that time HF–50 entered the nest with an inch-long insect with folded wings. She stopped in the entrance, and her tail could be seen bobbing up and down as though she were hammering at the insect in order to break it up. She then went inside and brooded for 13 minutes. At 6:07 p.m. the male entered and departed at once. Five minutes later HF–50 carried another insect inside the nest.

At 7:27 a.m. on the following day we found 3 nestlings; the fourth egg did not hatch. The male carried a worm about one-quarter of an inch long into the nest just before we inspected it. Our first observation period began at 8:21 a.m. and ended at 8:47 a.m. HF–50 brought food to the nestlings three times and brooded twice for 8-minute intervals. She was away from the nest 4 minutes each time. While she was brooding, the male visited her three times. The food he brought may have been given to her instead of the nestlings.

Resuming our watch at 9:58 a.m. we saw HF–50 enter nest 19C with food. She left almost at once. Then at 10:12 a.m. HM–54 arrived with what looked like a brown spider. He went inside, but came out in a few moments, still holding the object. Then he swallowed it and flew. Evidently there was no begging response at his entrance, so he could not dispose of the food. At this point there would seem to be a natural transition developing for the male, from courtship feeding to nestling feeding. The female took time out for 22 minutes. She now brooded for 9 minutes. Four minutes later she brought food again; then she brooded for 10 minutes. In the course of the next 13 minutes while she was away, the male brought food to the nest three times.

Our third observation period was from 3:30 p.m. to 4:10 p.m. At 3:35 p.m. HM–54 carried a small black insect to the nest; the female was absent. Again he must have failed to elicit a begging reaction, for he came out holding the insect. This time he flew away with it. HF–50 then came with food; she brooded 4 minutes. Eight minutes later, HM–54 returned with a small worm; he visited the nest again in 7 minutes. The female was absent about 25 minutes, then she brooded for 5 minutes.

We watched the nest again from 6:30 p.m. to 7:00 p.m., when HF–50 retired for the night. The male brought food twice, the female four times. Her brooding periods were now very short: 3, 1, 1.5 minutes; her periods away from the nest were 9, 3, 12 minutes.

On April 15, 1947, from 8:16 a.m. to 9:08 a.m., HF–50 fed the nestlings five times; the male came with food seven times. The female's brooding time was 6, 6, 11 minutes; her time off the nest was 5, 18, 6 minutes. On several of his visits, the male found the female inside the nest. The disposition of his food is doubtful again. He may have fed his mate. From 9:26 a.m. to 10:30 a.m. HF–50 brought food five times; the male came three times. The female's brooding periods were 0.5, 0.5, 10, and 2 minutes; her time off the nest was 4, 3, 22.5, 16.5, and 5 minutes.

These incomplete data for April 14 and 15 indicate that approximately 30 per cent of the time was devoted to brooding the young. The brooding intervals became very short in the late afternoon of April 14, and they were even shorter in midmorning of the 15th. Morning minimum temperatures were 42°F. on the 14th and 47°F. on the 15th. The afternoon maximum rose to 90°F. on the 15th. Even though body temperature regulation had probably not yet begun, the nestlings must have had little difficulty in keeping warm with a minimum of brooding by the female.

On April 16 brooding practically stopped after 9:00 a.m. The time which the female remained in the nest was hardly more than would be necessary to insure that the nestlings were properly fed. Occasionally a 3-minute period would be recorded, but most of the feeding periods could be expressed in seconds.

On April 19, 1947, the last-hatched nestling was five days old. We were able to ob-

serve the rate of feeding for the entire day, from the first visit to nest 19C at 5:38 a.m. to the female's retirement at 7:12 p.m. The hourly rates for both sexes in the course of this day are recorded in table 4. The sky was clear all day; we had light intermittent winds during the afternoon. The minimum temperature was 50°F., maximum 90°F., and mean 70°F. HF–50 averaged 7.3 visits per hour; HM–54 averaged 4.3 visits per hour. Brooding periods were observed three times in the early morning, of 16, 11, and

Table 4

Hourly Feeding Rate at Nest 19C on April 19, 1947

Time	HF–50	HM–54
5:38 a.m. to 6:38 a.m.	9	4
6:38 a.m. to 7:38 a.m.	3	4
7:38 a.m. to 8:38 a.m.	7	8
8:38 a.m. to 9:38 a.m.	5	2
9:38 a.m. to 10:38 a.m.	7	5
10:38 a.m. to 11:38 a.m.	7	3
11:38 a.m. to 12:38 p.m.	2	1
12:38 p.m. to 1:38 p.m.	9	6
1:38 p.m. to 2:38 p.m.	7	4
2:38 p.m. to 3:38 p.m.	8	4
3:38 p.m. to 4:38 p.m.	10	3
4:38 p.m. to 5:38 p.m.	7	4
5:38 p.m. to 6:38 p.m.	13	8
6:38 p.m. to 7:12 p.m.	5	2
Total visits with food	99	58

5 minutes duration. Inattentive periods, while seemingly very irregular in length, varied roughly to a peak 12 times during the day. There were 23 inattentive periods of 10 minutes or over, ranging from 10 to 30 minutes in which no feeding occurred. After each long absence or group of long absences, there followed a series of short ones, as the feeding rate increased.

Wheelock (1904:278) reported that nestling Cactus Wrens were fed by regurgitation for the first four days. We have found no confirmation of this anywhere else in the literature; in fact, there appear to be no direct observations at all on the early feeding procedure in any recent publication. This is not surprising, for nothing can be seen of the actual feeding after the adult enters the nest. We have described the feeding activities in every detail in an endeavor to show that the initial food of the nestlings is not delivered by means of regurgitation. The food consists of small, freshly-killed insects. Our male, when he brought food to the nest, probably gave it to his mate, if he found her inside. At other times, when the nestlings met him with open mouths, the natural thing to do would be to place the insect into the trembling, light-colored cavity. Both adults always brought visible, whole insects to the nest. The female could have chewed up her food while she brooded and then fed the nestlings, but sometimes the brooding period was far too short for this. The difficulty experienced by the male when he brought insects to the nestlings that were too large for them to swallow indicates that no mastication with subsequent regurgitation was contemplated. It was a case of take the food in its original condition or do without it. Our observations at a number of other nests confirm the fact that small insects are carried in the bill of the adult to the newly hatched young on the first three days of their life.

Flights to the nest were directly to the doorstep with no attempt at concealment. Flights from the nest also were apparently directly to the feeding areas, mostly east,

south, and west. Occasionally these flights were north over our house, but they did not go far in this direction, since it meant trespassing on another territory.

We observed the recognition display-growl at the nest four times in the forenoon on April 15. Three times it occurred when the male arrived at the doorstep and met the female coming out of the nest. On the fourth time, the male uttered the growl as the female alighted in front of him when he came out. This may have been a defensive or aggressive reaction as he was taken by surprise. Apparently HF–50 did not respond to the display, for HM–54 failed to move aside; she squeezed by him with some difficulty and crept into the nest with her food. By April 19 feeding of the nestlings had become a routine activity. If the male arrived when the entrance was blocked, he waited and stood aside just enough to permit his mate to leave. There seemed to be no sign of recognition or interest. At one of these visits he gave his food to HF–50, who turned around and carried it inside the nest. It all appeared so mechanical. In the course of the entire day not one display or growl occurred when the adults met at the entrance.

Singing by the male was more frequent during the forenoon of April 19. It tapered off in the afternoon and diminished rapidly after 6:00 p.m. It occurred usually after one or the other of the Cactus Wrens had fed the nestlings and left. Some of the songs may have been in response to activity in the adjacent territory I. Few songs, however, were noted during the long periods in which the adults took time to feed themselves. HF–50 sang a number of times at the nest entrance or near it when an immature Curve-billed Thrasher began digging in the ground beneath the cholla. Sometimes her song sounded very much like that of her mate; now and then the syllables were farther apart and possibly were pitched higher. The scratchy *scri* note was heard occasionally during the day, but we did not realize its significance until later, when we discovered that territorial disputes were taking place just north of our house.

The installation of lining material, which occurred so frequently during incubation, was seldom observed after the eggs hatched. At 7:56 a.m. on April 19, HF–50 carried some fine grasses to the nest; at 9:15 a.m. she brought feathers. In neither instance did she remain to brood.

In the course of our more limited observations up to April 19, we did not observe that any fecal sacs were removed from the nest. We presume that they were swallowed by the adults. On the 19th we saw the adults carry away sacs at the following times: 5:58 a.m., 6:13 a.m., 7:36 a.m., 10:46 a.m., 1:00 p.m., 1:05 p.m., 1:06 p.m., 4:29 p.m., and 4:40 p.m. These observations fall into four groups spaced roughly three hours apart. Both sexes took part in the disposal of these sacs. On the 25th HF–50 dropped a large fecal sac as she came out of the nest. The sac broke into fragments; then the female picked them up one by one and swallowed them. Our observations at other nests show that fecal sacs are removed from the nest up to the hour of fledging, and they are often carried as far away as 150 feet.

FLEDGING

When the nestlings in nest 6AJ in territory I were fledged on April 23, their parents led them into the north half of lot 7. Part of our attention now had to be directed to this group of wrens, leaving only brief intervals for observing the feeding at nest 19C in territory III. The boundary disputes which soon began must have disrupted to some extent the orderly routine at nest 19C.

As the nestlings grew larger they became more active. During their final week in the nest they climbed out of the nest cavity and into the vestibule where they awaited the arrival of food. While they were being fed, their individual begging notes were uttered so frequently that they merged into a loud, coarse buzz. On May 3, the day

before fledging, HM–54 sang with increased vigor in the vicinity of the nest. The nestlings crowded forward until one was outside the entrance when HF–50 came with food at 8:40 a.m. A warning *tek* note from the male sent the nestling back into the nest, but it did not stay there long. Soon two nestlings were out. The adult that came with food poked its head under one of the obstructing nestlings, raised its head and then pushed its way into the nest, evidently to feed the remaining one. It was difficult to keep them inside. For a while one of them squatted in the entrance, eyes closed, apparently asleep. Again they were wide awake, stretching their necks and peering about from the doorstep. At 9:41 a.m. one of the nestlings climbed to the top of the cholla; it came down part of the way when HF–50 arrived with food. The other two in the entrance were fed. HF–50 moved upward and sang just above the nestling, apparently in an attempt to induce it to climb down. This nestling was not fed until 20 minutes later when it had returned to the nest. No further excursions occurred up to 10:30 a.m., when we were forced to discontinue watching. For a short period the delivery of food had been at the very rapid rate of one visit per minute. Fledging probably took place some time after 7:00 a.m. on May 4. (We were absent most of the day.) On the 5th the three fledglings spent the entire day in the large mesquite tree 20 feet southeast of cholla 19.

Fledging at nest 25G was observed on March 25, 1958. At 9:00 a.m. singing had increased noticeably. HM–73 perched on a dead branch of the cholla near the nest. A nestling came to the entrance and looked around; then it retreated inside. This was repeated several times. HF–71 arrived with food, but instead of going to the nest, she stopped two feet away. Soon she flew to a nearby creosote bush; then she came back. Again she flew and returned, then she flew to cholla 4, about 15 feet to the south. The nestling which had been watching from the doorstep fluttered about a foot forward and landed on a cholla twig. It stayed there a few moments, balancing awkwardly among the sharp spines; then it flew downward to another twig. It hesitated and then flew upward another foot and teetered and hesitated again. The rapid singing continued from cholla 4. Finally the young wren flew to the base of this cholla in a curved, descending flight. A few minutes later a second nestling appeared in the entrance of nest 25G. It, too, advanced and retreated on the doorstep several times. Singing continued vigorously. Then the second fledgling, without any intermediate stops, suddenly followed the first in a direct flight to the base of the cholla 15 feet away. A third nestling then came to the doorstep, but it did not attempt to fly. The fourth also remained inside, and both were fed at the nest during the day. By 10:30 a.m. on the following day all nestlings were fledged.

It seems evident that at this period the song of the male takes on a new function. The singing, which occurred immediately after the feeding of the nestlings is difficult to explain. It was not usually uttered in response to the territorial song of adjacent rivals; it seemed to come spontaneously. At the time of fledging, however, the song appeared to be directed at the nestlings, and it served apparently as a signal for them to leave the nest and fly toward the singer. In the evening the same frequent singing led the fledglings back to their nest to roost for the night. The only difference that we can detect between this song and the territorial song is the more rapid rate of the former. There are more songs per minute; the shorter pauses permit little time for listening to any other songs.

The length of time which the nestlings spent in the nest, calculated from the day the first egg hatched until all the young had been fledged, varied from 19 to 23 days. The average of 13 nests was 20.9 days. The single nestling in nest 14C had been in the nest for 23 days when it left on March 21, 1945. In 1958 the three nestlings of the first brood remained in the nest for 23 days; two nestlings of the second brood left in 22

days, the remaining two on the next day; the five nestlings of the third brood left after 21 days. This does not indicate that late broods spend less time in the nest than do the earlier broods, for we have two records in March of 19 and 21 days. Fledging was accomplished in the course of one day in 14 nests; two nests required two days. Evidently the spread in time of fledging is not determined by the spread in hatching. Hatching was spread over three days in nest 5L in 1958, but all of the nestlings were ready to leave on May 5. Repeated disturbances, such as removing the nestlings for weighing and examination, did not cause early departure, provided they were discontinued several days before fledging. We feel sure that premature fledging occurred occasionally when people approached too close to the nests.

The intervals between the fledging of the young and the laying of the first egg of the second clutch show considerable variation. In 1945, fledging and laying occurred on the same day, but only one nestling was involved. The maximum interval was 13 days in 1940. The average for seven years is 6.8 days. Data for only four years are available for the interval between the second and third clutches. The minimum time was one day, the maximum 11 days, and the average six days. The year 1958, with the pair HM–73 and HF–71, can be summarized as follows: four days between the first and second clutch; one day between the second and third; three days between the third and fourth. After the failure of the fourth clutch, the pair of wrens built a new nest and laid after seven days. This, too, failed. Another nest was built and again the first egg was laid in seven days. The year 1959 (incomplete at this writing) with the same male, HM–73, but a new female, HF–86, progressed as follows: the interval between the first fledging and the second clutch was 10 days; the interval between the second fledging and the third clutch was 13 days. First laying occurred on February 19 in 1959 as against January 2 in 1958.

The time required for a successful nesting from the laying of the first egg to the fledging of the young averaged 38.4 days for 14 broods. The minimum time was 36 days, the maximum 41.

The environmental, physiological or psychological factors responsible for the termination of the breeding season are difficult to determine. Our data for 14 years, obtained from 16 territorial pairs, are striking in their variability and afford few hints for any conclusive answer. Three pairs of Cactus Wrens ceased breeding in May, four in June, two in July, six in August, and one in September. The season, measured from the laying of the first egg to the fledging of the last young, or the abandonment of the nest, varied in length from three to seven months, with the average at 4.4 months. This average appears to be an unsatisfactory figure, for the minimum length of season occurred when one or the other of a pair was lost. The acquisition of a new mate in the middle of the season did not always result in the initiation of another breeding attempt. We suspect that in the Tucson region the normal physiological decrease in sexual activity begins in the first half of July, after the daytime maximum temperatures have been maintained for several weeks at from 100°F. to 110°F. Eggs laid in early July produce young that are fledged in August. In 1955, 1956, 1957, and 1958, laying began respectively on March 12 and 7, February 21, and January 2. The breeding season was over on September 7, August 10, 13, and 3. Human activities in the neighborhood no doubt disrupted nesting attempts at times, but it is interesting to note that the longest breeding periods occurred in the past four years when the human population was the greatest. Perhaps the gradual restriction of the wrens to nesting sites in lot 7, where they were protected, is a factor here. Allan R. Phillips (personal communication) informed us that on September 20, 1938, Cactus Wrens were fledged from a nest near his home in the thickly populated university district of Tucson. Hensley (1959:90) found that

in the Organ Pipe Cactus National Monument in southwestern Arizona, the three month's breeding season extended from late March to late June. Since the late June date (Hensley, MS) refers to eggs laid and not to young fledged, the season in that area probably also ended in August.

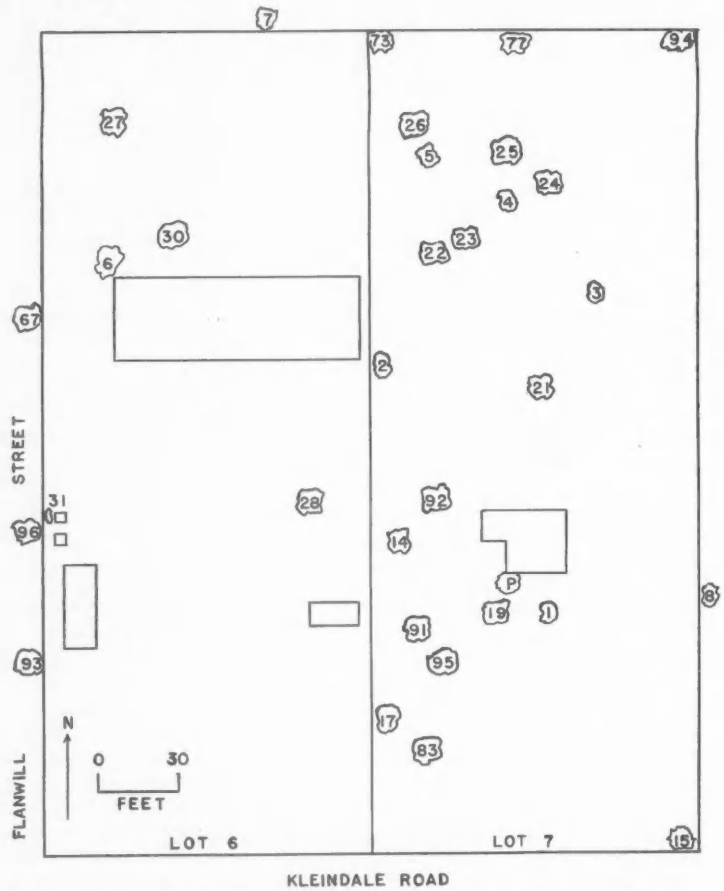

Fig. 2. Location of numbered cholla cacti in lots 6 and 7 along Kleindale Road, Tucson, Arizona.

SECONDARY NESTS

The literature on the Cactus Wren is filled with accounts of additional nests built in the vicinity of the breeding nest. Various terms have been applied to them, such as auxiliary, decoy, dummy, extra, shelter, spare, and supplementary, depending upon the use which the observer attributed to them. In view of the many conjectures and misstatements in the literature we are reporting in considerable detail the events of the year 1958, and we are summarizing our data for 13 of the annual nest building sequences

that we observed from the laying of the first egg to the fledging of the last young or its abandonment. The data for the remainder of the years listed in table 1 are too incomplete to be included here.

Normally, while the female incubated her eggs in the new breeding nest, the male began construction of one or more secondary nests. In figure 2 are shown the location of the numbered chollas in lots 6 and 7 on Kleindale Road in which the following data were secured. Unless otherwise stated, all the nests were in cholla cacti. In order to simplify the accounts, we have omitted our data on the nest-building activities of the immature Cactus Wrens. These will be described in a later paper.

Nest building in 1958 was almost entirely in lot 7, and it followed closely the main predictable pattern, with several interesting variations. Three wrens were present at the beginning of the year, HM–73, HF–71, and a noband. The male roosted in nest 5K, the female in nest 1I, and the noband in nest 21G. By January 2, HF–71 had moved into the male's roosting nest 5K in the northwest part of lot 7 and laid her first egg. HM–73, forced to find another nest, did not take over the female's roosting nest but began work on nest 21H on January 1 and gradually completed it. The noband wren which occupied nest 21G, only six feet away, was not seen after January 10. The secondary nest 25G, located 20 feet from the breeding nest, was begun on January 14. It appeared finished on the 24th. On February 9, HF–71 carried some lining material to nest 25G; HM–73 also worked on this nest. Fledging occurred on February 11. HF–71 squeezed into her old, weathered nest 1I that evening, for nest 5K was again crowded with the returned fledglings. She laid the first egg of her second clutch in nest 25G on February 15. The next day HM–73 began work on nest 83C in the south part of lot 7. He had given up his roosting nest to the fledglings and now retired temporarily in nest 5K. Later he occupied nest 83C. On March 1 this nest had a slightly torn entrance. HM–73 started nest 21I but soon abandoned it. The secondary nest, 5L, 14 feet from nest 25G, was not started until after March 15; it was well outlined on March 21, but lacked the interior lining. Nest 91G, found March 11 partly completed, probably was begun earlier and left in favor of nest 5L. HF–71 apparently roosted in nest 5L on the nights of March 23 and 24. Fledging from nest 25G took place on March 25. Two days later the first egg of the third clutch was laid in nest 5L. HM–73 completed nest 91G on March 30 and roosted in it; by April 10 he had repaired nest 83C also. This nest fell apart soon and was again repaired. Now the male gave up his roosting nest 91G to an immature wren and retired in nest 83C. Finally on May 4, HM–73 began construction of secondary nest 25H, just above the old breeding nest 25G. Fledging of the nestlings in nest 5L began the following day. The male worked rapidly on the new nest. The first egg of the fourth clutch was laid in nest 25H on May 8. On May 11, HM–73 began work on nest 5M, near nest 5L and again worked rapidly. On May 22 we discovered that he was roosting in a new nest, 96D, on Flanwill Street. Three of the eggs in nest 25H hatched, but on May 29 the nestlings had disappeared. After this failure the adults began construction of nest 17J in the south part of lot 7 on May 31. HF–71 roosted in nest 5K, HM–73 in nest 96D. On June 5 the first egg was laid in nest 17J. HM–73 began work on June 7 on secondary nest P4 in the large pyracantha bush beside our front door. Then he shifted his labors to another nest, 92D, near the northwest corner of our house, but he soon abandoned this one also. Incubation continued in nest 17J, but the eggs proved to be infertile. The nest was not occupied on June 29. The next day HM–73 and HF–71 joined in building nest 92D, which the male had tentatively started on the 10th. On July 4 the first egg of the sixth clutch was laid. The secondary nest, P5, located in the top of the pyracantha bush, was begun by HM–73 on July 8. He worked slowly on it, while he roosted in nest 96D. On August 3 the infertile

eggs in nest 92D were abandoned. The course of nest building in this most productive year is diagrammed in figure 3.

Secondary nests were occasionally begun as early as the day following the laying of the first egg of the first clutch. Normally we could expect to find them under construction from 8 to 14 days later. Destruction of roosting nests contributed to delays in starting these secondary nests. Greater delays sometimes occurred when the male was occupied in feeding a hungry group of three to five fledglings. Yet, even then, he sometimes managed to start a nest shortly after a clutch was complete. Nest 25H, in 1958,

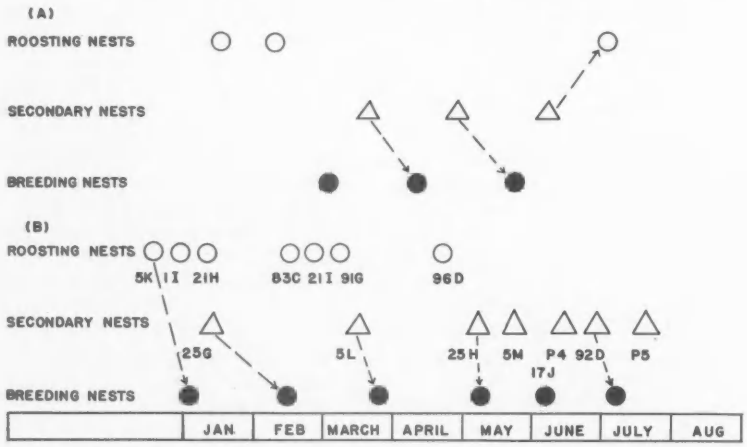

Fig. 3. A, "normal" nest-building sequence of Cactus Wren; B, 1958 nest-building sequence showing variations.

was begun the day before the nestlings were fledged from nest 5L, but the male had previously worked on two other nests. Milam Cater (personal communication) saw a male Cactus Wren begin a secondary nest on May 26, 1943; the following day this nest appeared completed. On the 28th another nest was begun by the male and finished by May 30, when the young were fledged from the breeding nest.

It was not unusual to discover that a secondary nest had been built in the same cholla that contained the breeding nest. Some nests were only a few feet away; others were back to back or a little above the primary nest (fig. 4). Locations elsewhere in the territory naturally depended upon the availability of nesting sites in cholla cacti. Distances from the breeding nest varied from 14 to 240 feet.

Secondary nests were well covered over and were sturdy and substantial in appearance in from 4 to 14 days. They often required more lining and additions to the entrance when the female moved in; for the work of the male had usually been interrupted by the necessity of assisting the female in feeding the nestlings. Only once did we see the female take any part in the construction of a secondary nest which the male had begun. After the fledging of her young, the female made her choice; then both adults finished the new breeding nest.

We have records of three temporary secondary nests that were built by females at the time their breeding nests were too crowded with nestlings to permit further night brooding. These nests were small and flimsy, but they served as roosting nests until the

young were fledged. Two of the nests were built just above the breeding nest; the third was at a distance of 160 feet from the breeding nest. In each of these three instances, other nests were available for roosting, but for some reason they were not chosen.

Under undisturbed conditions a secondary nest was always built by the male while the female incubated her first clutch. With but two exceptions this nest was a new nest. Nest 23F, in 1945, and nest 17M, in 1959, were started earlier in the year by the females and then abandoned. Later they were completed by the males.

In the course of the 13 breeding seasons, the male Cactus Wrens began construction

Fig. 4. Cholla 17 on March 1, 1959. Roosting nest 17J located at upper left, breeding nest 17L at upper right, and secondary nest 17M at top. Note the characteristic drooping joints of the cholla caused by lack of rain.

of a total of 59 secondary nests while the females were incubating, brooding, or feeding their nestlings. Some of these nests were not completed. If we omit the 23 nests which were begun during the last clutch of the year, and which obviously could only be used for roosting nests, we have 36 secondary nests available for use as breeding nests. Fifteen of these were chosen by females to be their breeding nests. The histories of the remaining 21 nests vary. Several were begun and then abandoned for no apparent reason to us; others were damaged by thrashers, and then a new one was started elsewhere. Some were certainly intended for roosting nests, since they were begun immediately after the destruction of the male's roosting nest. Such a nest was usually built hurriedly, with a secondary nest following before the young were fledged. Whenever the male, apparently willingly, gave up his roosing nest to the still dependent fledglings, he constructed another roosting nest for himself. We feel safe in stating that all completed secondary nests were occupied at some time by the male, the female, or the young wrens.

There were no nests that could be considered as decoys, and none that was superfluous. The rejection of a secondary nest by the female did not necessarily mean that there had been a waste of building time, for the fledglings soon needed enlarged roosting quarters. In fact, it is hard to avoid attributing to the Cactus Wren the ability to plan ahead!

Much more research is needed to determine what physiological requirements, if any, dictate the construction of roosting nests. It may be that such nests are not at all necessary in this mild climate. The Curve-billed Thrasher in the same spacial environment as the Cactus Wren, and a direct competitor for nesting sites, is able to hold its own, side by side with the Cactus Wren, without the aid of roosting nests. If roosting nests are necessary for the Cactus Wren, then it seems certain that secondary nests must have an important survival value.

SUMMARY

Cactus Wrens did not desert their nests when the entrances were disturbed and widened to facilitate inspection of the contents.

The females roosted in their breeding nests sometimes as much as 7 to 11 nights before the first egg was laid. Eggs were laid at the rate of one a day, on consecutive days in early morning. The average eggs per clutch was 3.41. Although as many as six clutches were laid in one year, the maximum number of broods raised was three. In four of the years three broods were raised; in nine of the years two broods were raised; and in four of the years one brood was raised.

Failure of clutches increased rapidly after the second clutch; all fifth and sixth clutches resulted in failure.

Incubation was performed entirely by the female. Partial incubation began the night after the first egg was laid; daytime incubation was irregular until the clutch was nearly complete. The period of incubation was found to be 16 days.

At one nest, on the seventh day of incubation there were 28 attentive periods averaging 14.8 minutes and 29 inattentive periods averaging 11.7 minutes each. The range of variation was 1 to 28 minutes and 2 to 26.5 minutes, respectively. On that day 54.9 per cent of the time was spent in incubation. The day before the first egg hatched, the female devoted 50.3 per cent of the time to incubation.

The female frequently carried lining material to the nest when she came to incubate. Courtship feeding by the male occurred three to four times a day.

Hatching of the eggs was spread over a period of two to three days. In no nest did all the eggs hatch on one day. About 30 per cent of the time was devoted to brooding during the first three days after hatching. The time decreased rapidly thereafter.

The feeding rate when the last hatched nestling was five days old was as follows: the female averaged 7.3 visits per hour, the male 4.3 visits per hour.

Nestlings are fed small fresh insects from the time they are hatched. Feeding by regurgitation was not observed. Fecal sacs were carried away from the nests when the nestlings were from five to eight days old.

As fledging time approached, the singing by the male Cactus Wren increased. The song appeared to be directed to the nestlings and apparently served as a signal for them to leave the nest. In addition the adults induced the nestlings to fly from the nest by stopping a short distance away and withholding their food.

The average time which the nestlings spent in the nest was 20.9 days; the range was from 19 to 23 days.

The first egg of the second clutch was laid in from 0 to 13 days after the fledging of the first brood; the average for seven years was 6.8 days. The interval between second and third broods averaged six days; the range was one to 11 days.

The time required from the laying of the first egg to the fledging of the young aver-

aged 38.4 days for 14 broods; the maximum was 41 days, the minimum 36 days. Normally in the Tucson region, the breeding season probably ends with the fledging of the last young in the middle of August. Our local birds varied the length of the season from three to seven months.

Each year began with a minimum of two roosting nests. Both adults constructed the first breeding nest. While the female incubated the eggs the male began construction of one or more secondary nests. Some were begun as early as the day following the laying of the first egg; most were begun eight to 14 days later. Sometimes these nests were placed close to the breeding nest in the same cholla; others were from 14 to 240 feet distant. The female did not assist in their construction until after the young were fledged. She then laid her next clutch of eggs in the secondary nest. Variations in this "normal" behavior were rather common. Occasionally the female appropriated her mate's roosting nest for her next clutch. After a clutch failure she sometimes ignored the secondary nests and, with the help of the male, constructed an entirely new nest for her eggs. Rarely she laid her next clutch in the same nest that housed the previous brood. Frequently these secondary nests were built as replacements of destroyed roosting nests. Three of the nests were built entirely by females whose breeding nests were too crowded with nestlings to permit comfortable night brooding; they should probably not be classed as secondary nests.

None of the secondary nests could be termed "extra" or "decoy." All the completed ones served some useful purpose. Those that did not become breeding nests were used by the male, the female, or the fledglings for roosts.

LITERATURE CITED

Anderson, A. H., and Anderson, A.
1957. Life history of the cactus wren. Part I: Winter and pre-nesting behavior. Condor, 59:274–296.
1959. Life history of the cactus wren. Part II: The beginning of nesting. Condor, 61:186–205.
Bent, A. C.
1948. Life histories of North American nuthatches, wrens, thrashers and their allies. U.S. Nat. Mus. Bull. 195.
Brandt, H.
1951. Arizona and its bird life (The Bird Research Foundation, Cleveland, Ohio).
Enemar, A.
1958. Om ruvningens igångsättande hos koltrast (*Turdus merula*). Vår Fågelvärld, 17:81–103.
Heinroth, O.
1922. Die Beziehungen zwischen Vogelgewicht, Eigewicht, Gelegegewicht und Brutdauer. Jour. für Ornith., 70:172–285.
Hensley, M. M.
1959. Notes on the nesting of selected species of birds of the Sonoran desert. Wilson Bull., 71:86–92.
Swanberg, P. O.
1950. On the concept of 'incubation period." Vår Fågelvärld, 9:63–80.
Wheelock, I. G.
1904. Birds of California (A. C. McClurg and Co., Chicago).

Tucson, Arizona, July 15, 1959.

THE WHISTLING SWAN IN THE WEST WITH PARTICULAR REFERENCE TO GREAT SALT LAKE VALLEY, UTAH

By GLEN A. SHERWOOD

The Whistling Swan (*Olor columbianus*) has been increasing noticeably in the Pacific flyway through the 11-year period up to 1958. They continued to increase in 1958 and reached a recent high of 49,946 individuals for the Pacific flyway states (minutes of meeting of Pacific Flyway Council, 1958).

Paralleling the rise in numbers of Whistling Swans has been a mounting interest in the bird by many groups and individuals. This interest has taken various forms, from purely aesthetic to a deep concern over what effect the increasing swan population will have on other waterfowl; and, further, the United States Fish and Wildlife Service has been urged to allow an open hunting season on this species (minutes of meeting of Pacific Flyway Council, 1957). Because of these factors, it was believed that a study of the species might afford a worthy contribution to the literature on this swan.

THE STUDY AREAS

The main study area was located at the Bear River Migratory Bird Refuge, 15 miles west of Brigham City in northern Utah. Bear River Refuge consists of about 64,000 acres and is situated on the delta of the Bear River where it flows into Great Salt Lake (Fish and Wildlife Service, 1952). Lesser portions of the study were carried on at Ogden Bay and Farmington Bay refuges on the eastern shores of Great Salt Lake, Utah.

POPULATION OF THE WHISTLING SWAN

The continental population of Whistling Swans has been fluctuating since 1952, but it has been constantly dropping since 1955, when the total population was about 123,000 (Stewart and Manning, 1958; Crissey, 1957, 1958). At the same time the population of western swans has been generally increasing to the high in 1958 of 49,946 (fig. 1). However, John E. Chattin (personal communication) reports that the count in January, 1959, showed a drop to 39,599 in the Pacific flyway. Conversely, in 1958, the Atlantic population fell to a new low of about 27,900 (fig. 1). One can only speculate as to whether these fluctuations in the two populations are due to changing migrational patterns, to some breeding ground phenomena, or to mortality factors operating in one area and not in another.

The concentration areas of Whistling Swans for 17 western states, during fall migration and on the wintering grounds, are shown in figure 2. Northward migration in the spring shows a somewhat similar pattern of distribution. An interesting question brought to light is that of the direction of migration of swans upon leaving North Dakota in the fall, as the great majority do not go due south; their migration must be either to east or west. An extensive banding program might afford the answer.

The Bear River Migratory Bird Refuge in northern Utah annually harbors one of the largest, if not the largest, single concentrations of Whistling Swans in North America. The birds usually arrive at the Bear River Refuge in the second week of October and reach peak numbers in the latter part of November. If weather conditions do not become severe, substantial numbers of swans winter there. It is not uncommon to see large numbers of them loafing on the ice or moving about in small pockets of frigid water. The Whistling Swans depart from Bear River Refuge to the north in April and early May. Since 1946 the swan population at Bear River has fluctuated from

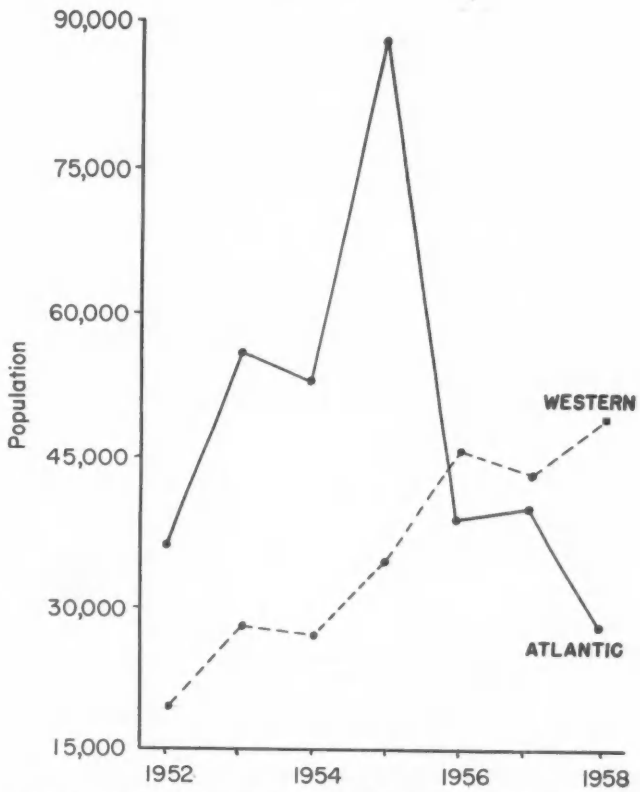

Fig. 1. Fluctuations of populations of the Whistling Swan of the Atlantic coast and western United States from 1952 to 1958. From Stewart and Manning (1958) and Crissey (1957, 1958).

a low of 6975 in 1948 to a high of 22,500 in 1955. In 1957 the fall peak was 18,150, and in 1958 it was 11,625 (Bear River Refuge census figures). The population at the refuge is not necessarily indicative of that of the Pacific flyway (table 1).

FOOD HABITS

The food requirements of the Whistling Swan in Great Salt Lake Valley are comparatively simple. The crops and gizzards of 50 swans were examined for food content. Many specimens could not be used for a food habits study because the gizzards and proventriculi contained no food or because the bird had died of some cause which might have altered its natural habits before death. Twelve (24 per cent) of the 50 swans examined were considered suitable for the study, and all 12 had been feeding exclusively on tubers and seeds of sago pondweed (*Potamogeton pectinatus*). At Bear River Refuge and Ogden Bay Refuge the swans feed almost exclusively in the open water areas, and in these areas the most abundant vegetation was sago pondweed. Ditch-grass (*Ruppia*

maritima) and horned pondweed (*Zannichellia palustris*) were available in some of the open water areas, but these were apparently not used by the swans.

Although swans can walk with apparent ease I have never observed them grazing in fields upon agricultural crops.

COMPETITION

The Whistling Swan's feeding habit of tearing up tubers and roots and creating pockets in the mud has been condemned by some people and has been considered by

Table 1

Whistling Swan Population at Bear River Refuge and in the Pacific Flyway States, 1952–1958*

Year	Pacific flyway states winter inventory (Jan.)	Bear River Refuge, peak fall population (Nov.)
1952	19,400	14,100
1953	28,200	14,500
1954	27,100	16,900
1955	35,000	22,500
1956	46,000	10,000
1957	43,000	18,150
1958	49,900	11,625
1959	39,600	———

*Winter inventory figures from Stewart and Manning (1958) and Crissey (1957, 1958). Bear River Refuge population from the refuge's census figures.

others as an aid to waterfowl. Bent (1925:286) reported that Whistling Swans "do considerable damage by treading great holes in the mud and by rooting and pulling up the celery and grass; they thus waste large quantities of these valuable duck foods, much more than they consume, and consequently spoil some of the best feeding grounds for ducks, much to the disgust of the sportsmen." Further, Bruette (1930) stated that the swans "are primarily vegetable feeders, and so voracious that they lay waste much of the feeding ground suited to ducks. They pull up the celery, root and branch, taking more than they require and leaving it floating useless on the surface of the water."

Personnel at Bear River Refuge feel that competition with other waterfowl, if any, is not serious. Further, they are convinced that swans are not a detriment to ducks but rather a help because they pull up more food than they need and this excess is used by the ducks. The food probably would not otherwise have been available to the dabbling ducks because of water depth. There is a possibility that the swans' feeding activity may create the establishment of new sago beds by dissemination of seeds and tubers and by "cultivation" of the marsh bottom.

Wherever I have seen Whistling Swans feeding I have also observed ducks and geese with them and following them, and often members of these species number in the hundreds. Many times I have seen flocks of Great Basin Canada Geese (*Branta canadensis*), Snow Geese (*Chen hyperborea*), Mallards (*Anas platyrhynchos*), Pintails (*Anas acuta*), Gadwalls (*Anas strepera*), Canvasbacks (*Aythya valisineria*), Redheads (*Aythya americana*), and Buffleheads (*Bucephala albeola*) feeding among the swans. The swans display no visible intolerance to these other waterfowl. If any depletion of forage is brought about by the Whistling Swan it is probably not great, because for years waterfowl of all species have been returning, in numbers of up to 1,000,000 to the Bear River Refuge without apparent damage to the vegetation.

MORTALITY FACTORS

The Whistling Swan is a legally protected bird, yet one-half (50 per cent) of 58 swans examined were killed with shotguns (table 2). Illegal shooting of the Whistling Swan is not new. Moffitt (1939) pointed out that as many as 300 are illegally shot in California each year, and Floyd Thompson, Federal Game Agent (personal communication) reports that nearly as many are shot in Utah every fall. The Whistling Swan is particularly vulnerable because of its habit of flying low across the marshes, and every hunter is undoubtedly tempted when such a target is presented, but this does not excuse their indiscriminate shooting.

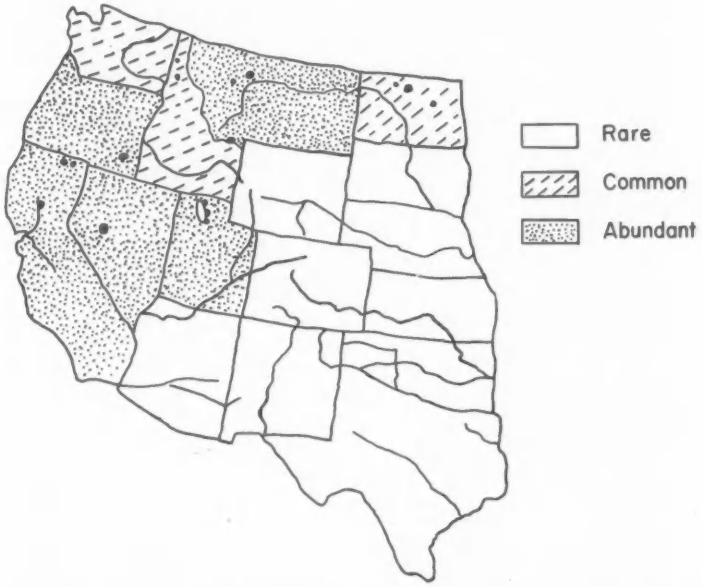

Fig. 2. Concentration areas of the Whistling Swan during fall migration and on wintering grounds for 17 western states. Data acquired from questionnaire sent to state Game and Fish departments and to refuge managers and federal game agents in regions 1 and 2 of the United States Fish and Wildlife Service. Rare, 0–400; common, 400–5000; abundant, 5000–35,000.

Eighteen swans which showed no evidence of gunshot wounds were fluoroscoped (fig. 3). Seven (38.9 per cent) of the 18 had a total of 18 lead pellets in their bodies. Two swans had five shots each, one had four, and four birds had one shot each. The shots were located in various portions of the body including abdomen, head, back, breast, wings, and neck. Shot size ranged from numbers 2 to 5.

Lead poisoning, which annually takes a toll from other waterfowl (Jordan and Bellrose, 1951), has also killed Whistling Swans. The swan's ability to dig deeply into the marsh bottoms might possibly allow them to pick up and ingest lead shot more readily than do other waterfowl. Ten of the 58 swans examined in this study definitely had died of lead poisoning (table 2). Some of them had ingested fantastically large numbers of

shot. One swan examined had ingested 236 pellets. Strangely, all 10 birds involved were juveniles. Several of the 10 had a food impaction from the gizzard to the throat opening. Paralysis of the gizzard is an effect of lead poisoning.

Disease, botulism, and unknown causes ranked second as a group of mortality factors, claiming the lives of 16 of 58 Whistling Swans examined (table 2). Eight of the 16 died of unknown causes. Of the remaining eight swans, three probably died of

Table 2

Mortality Factors of Whistling Swans from Great Salt Lake Valley, Utah, 1957–1958

Cause of death	Number	Per cent
Gunshot	29	50.0
Lead poisoning	10	17.2
Disease, etc.	16	27.6
Accidents	3	5.2
Total	58	100.0

botulism; three succumbed to aspergillosis; one died from tuberculosis; and one died of coccidiosis. Since completion of this study, I have been informed that about 40 Whistling Swans died at Bear River Refuge in late February and early March of 1959. Botulism was suspected, but conclusive evidence was unavailable.

Accidents killed three of the 58 birds examined. One large male (19 lbs. 10 oz.) apparently crashed into a dike at Bear River Refuge during a hail storm on March 25, 1958. A juvenal female swan was found near Ogden Bay Refuge on February 26, 1958, with the lower mandible torn away. Probable cause of this was a muskrat trap. The third swan that succumbed to an accident died of complications from a compound wing fracture.

Except for the one swan that died of coccidiosis, parasites probably did not directly cause death in any of the other 27 birds examined for parasites. The parasites may have been secondary causes of death in some cases. All 28 swans, however, were infected with parasites to some degree, and four were severely infected.

POTENTIAL STATUS OF THE WHISTLING SWAN AS A LEGAL GAME BIRD

Some individuals and groups have been requesting that the United States Fish and Wildlife Service allow a limited open season on the Whistling Swan (Pacific Flyway Council Meeting, 1957). Supporters of this program give the increasing swan population as one reason for allowing the harvest. Others feel that the swan is competing with other waterfowl for food and space, and thus their numbers should be reduced. Still others consider the swan a resource which could supply hunting pleasure.

There are, however, many biologists and bird lovers who are convinced that such an open season would not be wise management. Their arguments include: not enough birds, confusion with the Trumpeter Swan (*Olor buccinator*) and Whooping Crane (*Grus americana*), low table value, and high aesthetic value.

In the winter of 1957–1958 a questionnaire was sent to the 18 western game and fish departments and to the refuge managers and game agents in regions 1 and 2 of the United States Fish and Wildlife Service asking if they would favor a liimted harvest of the Whistling Swan. Of the 17 western states responding, five (29.4 per cent) favored an open season on the Whistling Swan, eight (47.1 per cent) were opposed, and four (23.5 per cent) expressed no opinion. Further, among personnel of 17 national

wildlife refuges answering, three (17.6 per cent) favored an open season, and 14 (82.4 per cent) did not. Similarly, of 11 federal game agents reporting, one (9.1 per cent) favored the harvest, nine (81.9 per cent) did not, and one (9.1 per cent) expressed no opinion.

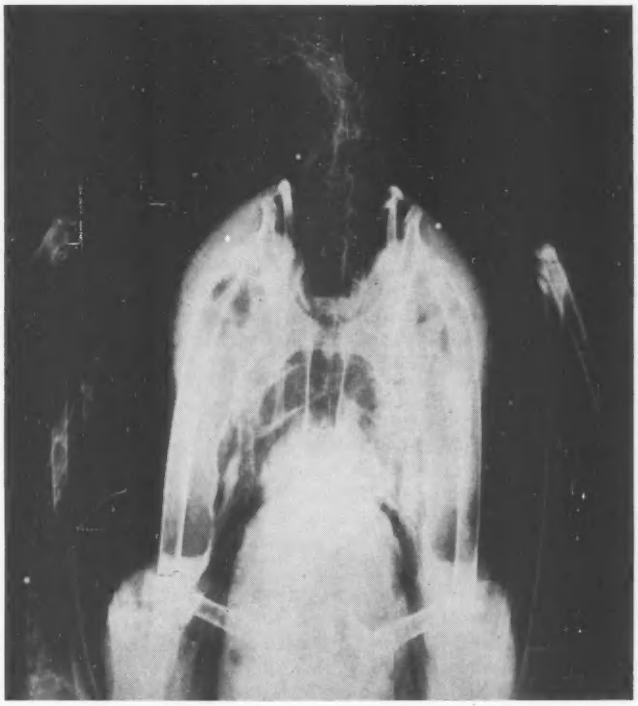

Fig. 3. X-ray of Whistling Swan showing lead shot (white dots) in neck and breast; December, 1958. Photograph courtesy of Budge Clinic, Logan, Utah.

It was my conclusion that a limited harvest of the Whistling Swan is not to be recommended for the following reasons:

1. The swan population is not increasing in North America. It has increased in the west up to 1958, but it fell considerably in 1959, and the Atlantic population was drastically down in 1958.

2. As swans do not mate until their third or fourth year, many juvenal swans would be shot before they reached the breeding age (Kortright, 1942).

3. Because of the bird's large size, the crippling loss from a hunt could account for additional reduction in swan numbers.

4. The fact that a few favored locations in the United States harbor large concentrations of the Whistling Swan is not enough justification to allow a hunt. There are many areas where Whistling Swans are rare. A harvest would further reduce the opportunity of observing the magnificent flights of these birds.

5. The Trumpeter Swan population would undoubtedly be placed in jeopardy if a harvest of the Whistler is permitted. Further, even though the Whooping Crane and Whistling Swan ranges overlap but little, it is not inconceivable that hunting the Whistler could mean occasional accidental shooting of a Whooping Crane.

6. That the Whistling Swan is creating severe competition to other waterfowl for food and habitat has not been proved.

7. Whistling Swans would not be favored for their table value as they are considered very tough. Bruette (1930) stated that "as game birds, they are not especially valuable because their long life toughens them and renders them practically useless as food. The younger ones, though, are fair eating when in good condition."

8. The aesthetic value of the swan is considerable, probably greater than that of any other waterfowl. The Whistling Swans make their contribution in beauty and should not become a game bird.

ACKNOWLEDGMENTS

Many individuals contributed their time and efforts to this study. In particular, however, I wish to thank Dr. Jessop B. Low of the Utah Cooperative Wildlife Research Unit, and Dr. Malcolm E. McDonald of the Bear River Research Station for extensive help and encouragement. I am also indebted for financial support to Mr. and Mrs. James C. Bertelson of Missouri Valley, Iowa, to the American Museum of Natural History, and to the Utah Cooperative Wildlife Research Unit.

SUMMARY

The population of swans of the western or Pacific flyway increased to a high of 49,946 in 1958. However, the count of January, 1959, showed a drop to 39,599. The Bear River Refuge, 15 miles west of Brigham City, Utah, annually harbors one of the largest concentrations of Whistling Swans in North America. Population figures at the refuge ranged from a low of 6975 in 1948 to a high of 22,500 in 1955. In 1958 the fall peak was 11,625.

The food habits of the Whistling Swan in Great Salt Lake Valley are simple in that they feed exclusively on sago pondweed.

Competition between the Whistling Swan and other waterfowl for food and habitat was not considered serious at Bear River Refuge.

Mortality factors affecting the swans in Great Salt Lake Valley, Utah, include gunshot, lead poisoning, disease, and accidents. Twenty-nine birds of 58 examined were found to be carrying lead shot in their body tissues.

The majority of the biologists, game agents, and refuge managers queried about the possibility of hunting the swans were opposed to such a program.

LITERATURE CITED

Bent, A. C.
1925. Life histories of North American wildfowl. U. S. Nat. Mus. Bull. 130.

Bruette, W.
1930. American duck, goose and brant shooting (Charles Scribners and Sons, New York).

Crissey, W. F.
1957. 1957 status report of waterfowl. U. S. Dept. Int., Fish and Wildlife Service, Spec. Sci. Rept.: Wildlife No. 37 (Washington).
1958. 1958 status report of waterfowl. U. S. Dept. Int., Fish and Wildlife Service, Spec. Sci. Rept.: Wildlife No. 40 (Washington).

Fish and Wildlife Service
1952. Bear River, a national wildlife refuge. Refuge Leaflet 2 (U. S. Government Printing Office).

Jordan, J. S., and Bellrose, F. C.
1951. Lead poisoning in wild waterfowl. Illinois Nat. Hist. Surv., Biol. Notes No. 26.
Kortright, F. H.
1942. The ducks, geese and swans of North America (American Wildlife Institute, Washington, D. C.).
Moffitt, J.
1939. Notes on the distribution of the whistling swan and Canada goose in California. Condor, 41:93–97.
Stewart, R. E., and Manning, J. H.
1958. Distribution and ecology of whistling swans in the Chesapeake Bay region. Auk, 75:203–212.

Utah Cooperative Wildlife Research Unit, Utah State University, Logan, Utah, March 21, 1960.

AGONISTIC BEHAVIOR IN THE HOUSE FINCH
Part II: FACTORS IN AGGRESSIVENESS AND SOCIALITY

By WILLIAM L. THOMPSON

In the first part of this paper (Thompson, 1960), the main features of the annual cycle of behavior of wild House Finches (*Carpodacus mexicanus*) were described. This part is concerned with dominance and related factors in sociality and with the possible relations of social organization to populations in the field.

Methods and materials were discussed in Part I (Thompson, 1960). In this part, numbers of tables and of figures continue the series of Part I.

SPATIAL AND SEASONAL ASPECTS OF AGGRESSIVENESS

The problem of the effect of space on the frequency of aggressive encounters was approached by varying the number of pairs of birds confined in a constant space. One, two, three, and four pairs of House Finches were placed in four equal-sized cages with dimensions of 4×8×8 feet. Each group was watched for one hour each day between 8 a.m. and 12 m. for four consecutive days, from February 4 through 7, 1959. The time of observation was rotated, so that each cage was observed at a different time on different days. This rotation was intended to minimize variations in the morning activity cycle. Figure 7 illustrates the results of this experiment. If the space available per bird is calculated by dividing the total space in the cage by the number of birds, it is apparent that fighting increases as space decreases. The increase of fighting with increased population density is not directly proportional to the space reduction, however, but it increases sharply where there is less than 60 cubic feet of space per bird.

Aggressive action occurs more frequently among caged birds than it does in wild birds. This may result from the reduction of space available per bird and from the increased frequency of contact between individuals. Between February 10 and March 19, 1959, records of aggressive encounters between wild House Finches were compared with records of such encounters between 11 birds confined in one cage for the same period. House Finches often congregated in an isolated elderberry tree on the study area, and because of the ease of observation the records of aggression among wild birds were taken from observations of birds in this tree.

The total number of encounters between wild individuals recorded during 8.25 hours of observation was 83, or 10.1 encounters per hour. For the caged birds the total number of encounters recorded during four hours of observation was 145, or 36.2 encounters per hour. The picture is greatly complicated by the varying numbers of wild birds present during any period of observation. If the maximum number present during five-minute intervals throughout the period of observation is recorded, it is possible to arrive at a fairly accurate figure for the mean number present throughout the time of observation. This calculated mean is 4.5 individuals. If we assume that the space available to these birds is equal to the volume of the portion of the tree used by the House Finches, roughly the upper half or 1188 cubic feet, the space available for each bird is roughly 264 cubic feet. Comparison of these numbers with figure 7 shows that they fall within the range of variation which might be expected if the curve were extrapolated. The curve should be thought of not as a single line but as a band which allows for some variation in the number of aggressive encounters which occur at any one concentration of individuals within a given space. There are still too many uncontrolled variables involved in the relationship between density and the amount of aggression to allow the construction of a precise curve to illustrate this relationship. Much more work is needed to clarify the issue. The evidence obtained from caged and wild House Finches

does, however, suggest that the greater aggressiveness of caged birds is associated with the decreased amount of space available to them.

Annual variation in frequency of agonistic behavior of nine caged birds in 1954–55 and eight in 1957–58 is shown in figure 8. The tallies of aggressive encounters on which these figures are based were obtained in the course of observations originally intended merely for determining the dominance hierarchy. Because of this the observation sessions were not always of the same length. For the purpose of obtaining the range of variation in number of encounters recorded during any one four-week observation period

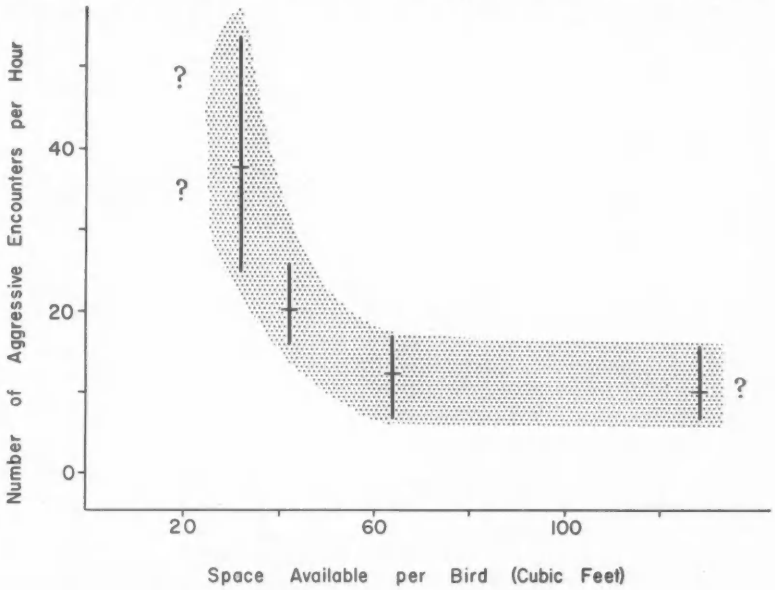

Fig. 7. Decrease of aggressive behavior of House Finches with decrease of population density within cages. Vertical lines indicate the range of total encounters per hour during four one-hour observation periods. Cross bars represent the mean number of encounters per hour.

it was necessary to adjust each observation session to a standard period of time. Since the greatest activity usually occurred near the beginning of the observation session at the time the birds were fed fresh vegetable material, it was decided that an adjustment of each session to a period of 20 minutes did less violence to the original data than expansion of some of the shorter sessions to one hour. Although the patterns of variation shown for the two years differ, the general trends are the same, with peaks in late fall, a marked depression in February, the suggestion of a second peak in early spring, and another depression in late May and early June. The longer record for 1958 suggests a third peak in late June, followed by a depression in July and August. The correspondence of these fluctuations in two different groups of birds in two separate years is considered significant. The most obvious cause for the seasonal fluctuations would be weather, but figures 9 and 10 suggest no correlation of agonistic behavior with either precipitation or temperature.

There is another possible cause of the marked drop in the number of aggressive encounters recorded in certain intervals. At about the end of January and in early February, continuing on through March, there is an increased degree of restlessness, taking the form of aimless flying back and forth from perch to perch, corresponding to the "Zugunruhe" of migratory birds. Possibly some of the caged birds were winter residents

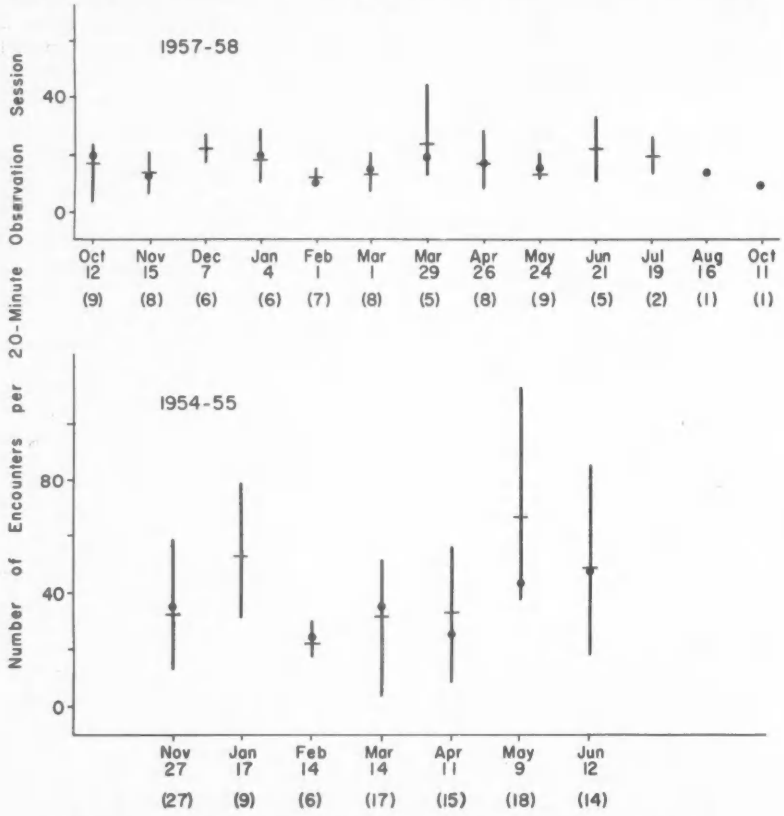

Fig. 8. Seasonal variation in the total aggressiveness of all caged birds, 1954–55, 1957–58. Vertical lines represent the range of total encounters per twenty-minute observation session. Cross bars represent the mean number of encounters per twenty minute session, and dots represent the mode. Dates represent the midpoint of four-week observation periods. Numbers in parentheses indicate the number of adjusted obsertion sessions (for explanation see text).

in the Berkeley area, which would have moved to distant localities during the spring. Or it may be that this activity is merely an expression of a dispersal mechanism which tends to break up winter flocks and scatter the birds for breeding. The movement of wild birds at this time of year is documented by the increased numbers of unbanded birds which appear at feeding stations usually frequented by marked individuals. At

any rate, this extreme restlessness masks aggressive encounters between birds. The observer experiences great difficulty in recognizing such encounters amid the frantic flying about. The February dip may, therefore, be "unreal" in terms of the actual occurrence of aggressive encounters at this time.

The cause of the June depression is not apparent. It may also reflect a wandering tendency on the part of adults after the first brood has left the nest. This, also, was indicated in the virtually complete absence of House Finches from the study area, where they had been so abundant, during late May and early June.

Table 3[1]

Distribution of Wins Throughout the Test Groups in 1954–55 and 1957–58

Midpoint of observation period	Total wins	Number of individuals responsible for:					
		25 per cent		50 per cent		75 per cent	
		♂	♀	♂	♀	♂	♀
1954–55							
Nov. 27	989	1	1	1	2	3	3
Jan. 17	470	1	1	1	2	3	3
Feb. 14	300		1	1	1	3	3
Mar. 14	1133	1		2		2	2
						or 3	1[2]
Apr. 11	1023	1		2		2	
May 9	1981	1		1		2	
June 12	1733	1		1		2	
1957–58							
Oct. 12	457		1		2		3
Nov. 15	323		1		2		4
Dec. 7	202	1	1	1	2	1	3
Jan. 4	195		2		3	1	4
Feb. 1	148		1		2	1	3
Mar. 1	193	1		1	2	2	3
Mar. 29	197	1		1	1	2	3
Apr. 26	246	1		1	1	2	2
May 24	185	1		1		1	2
June 21	165	1		1		1	1
July 19	58	1		1		1	1
Aug. 16	40	1		1		1	1
Oct. 11	50		1	1	1	1	1

[1] Tables 1 and 2 appeared in Part I of this paper.
[2] During this period a male and a female were tied for fourth place.

There is a marked difference in the number of aggressive encounters recorded in the two years. The peaks in 1955 are much higher than in 1958. There was one more bird in 1955 than in 1958; and, moreover, differences in individual aggressiveness would be expected apart from those induced by difference in group size. Another factor is difference in cage size. The effect of crowding on the incidence of agonistic behavior has already been mentioned. It is possible that some differences are also due to cage location. In 1955 the cage, although covered by a roof and exposed to direct sunlight only a short time each day, was in much brighter surroundings than the cages of 1957–58, which were located under oaks and were partly shaded throughout the day. Wild House Finches usually stay in the tops of trees and feed in open areas, avoiding the deep shade of dense woods. The cages of 1957–58 were therefore in a suboptimal habitat.

A bird is said to win an encounter if it causes its opponent to retreat. If all members of a group of eight caged individuals were equally aggressive, two, four, and six indi-

viduals would be responsible for 25, 50, and 75 per cent, respectively, of the total number of aggressive encounters recorded for a given period of time. It is possible to obtain some measure of how the test group conforms to or departs from this distribution. Table 3 shows the distribution of wins throughout the test groups in 1954–55 and 1957–58. During November and January of 1954–55 the figures agree closely with the

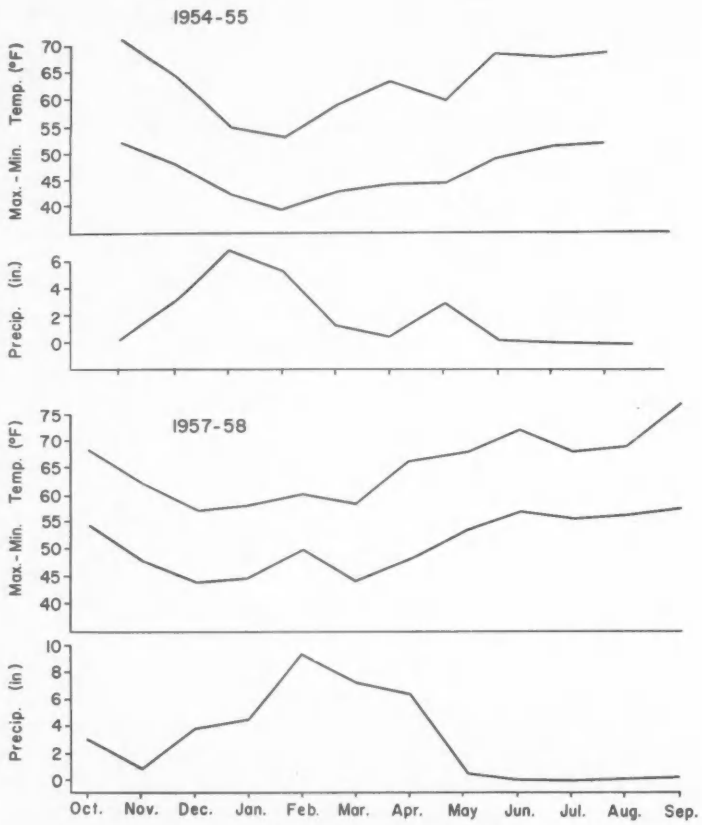

Fig. 9. Weather data for 1954–55 and 1957–58.

expected distribution. The ratio 2:3:6 is well within any variation which might be expected on the basis of chance. The June distribution, on the other hand, is radically different. At this time one individual is responsible for 50 per cent of all wins, and two are responsible for 75 per cent of all wins. Likewise in 1957–58, the October-November distribution is not far from the expected ratio. The prominence of females in aggressiveness within a caged group is noteworthy in 1954–55. In the spring one male is responsible for 50 per cent of all wins, and the male and his mate for 75 per cent of the total, as in 1954–55. It is clear, then, that the increase in the total aggressiveness of the group

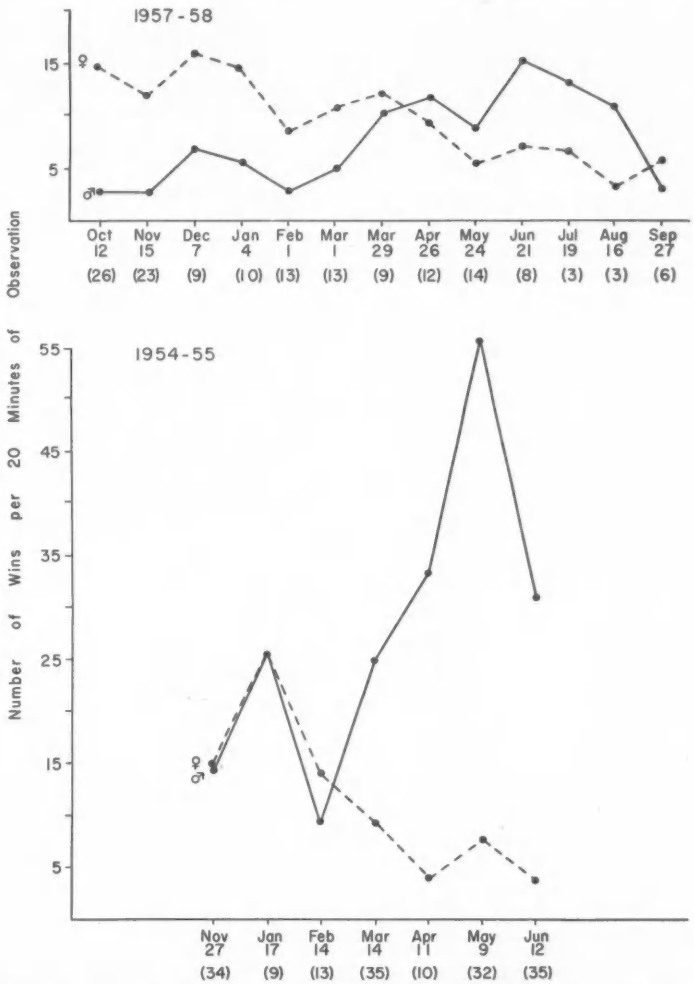

Fig. 10. Seasonal variation in the total aggressiveness of nine caged male and female House Finches in 1954–55 and eight caged males and females in 1957–58. Numbers in parentheses indicate the number of 20-minute observation sessions per four-week period.

during the breeding season is due primarily to an increase in the aggressiveness of a few individuals rather than of the group as a whole (see also fig. 13).

A breakdown of the data on total aggressiveness into male and female components indicates the varying roles of the two sexes throughout the year. In these data, shown in figure 10, the total time of observation is divided into 20-minute segments instead

of adjusting each of the observation sessions to a 20-minute period. The number of wins per 20 minutes of observation is then calculated. Again the graph for 1955 is the more striking because of the great increase of male aggressiveness in spring. A corresponding increase of male belligerence and a simultaneous decrease in female hostile behavior was found in 1958, but to a much smaller degree than in 1955. This rise of male aggres-

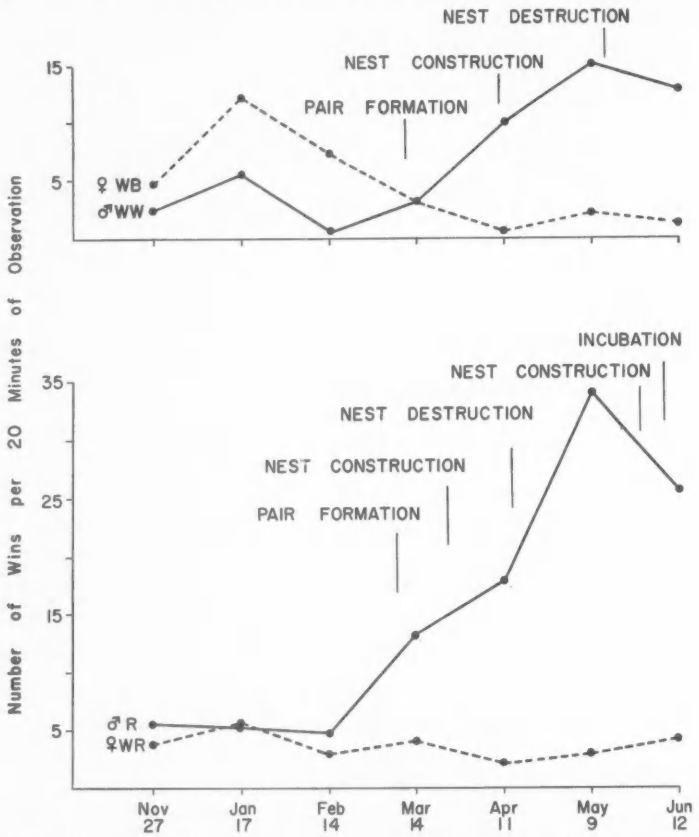

Fig. 11. Seasonal variation in the aggressiveness of two caged pairs of House Finches in 1954–55. The times of pair formation and other events in the annual cycle are indicated.

siveness is undoubtedly related to the defense of mate and territory. A male becomes most aggressive when his mate is building a nest and beginning incubation. This may be observed in wild as well as in captive pairs. It is very noticeable in a cage, when the male whose mate is nesting begins to chase all the other birds in the cage, except his mate, as if defending a territory. Whereas previously he might supplant another male only if it was in his way on a perch, he now makes long detours to supplant subordinate males. This increase of male aggressiveness with sexual activity is illustrated in fig-

ures 11 and 12, in which the hostile activity of active pairs in 1954–55 and 1957–58 is diagrammed. In almost every case there is a marked increase in fighting from the time of pair formation. Another increase is noticeable (with the exception of male WP) at the time of nest construction and the beginning of incubation. These increases accord well with the increases in fighting observed in the wild. The apparent reason for the

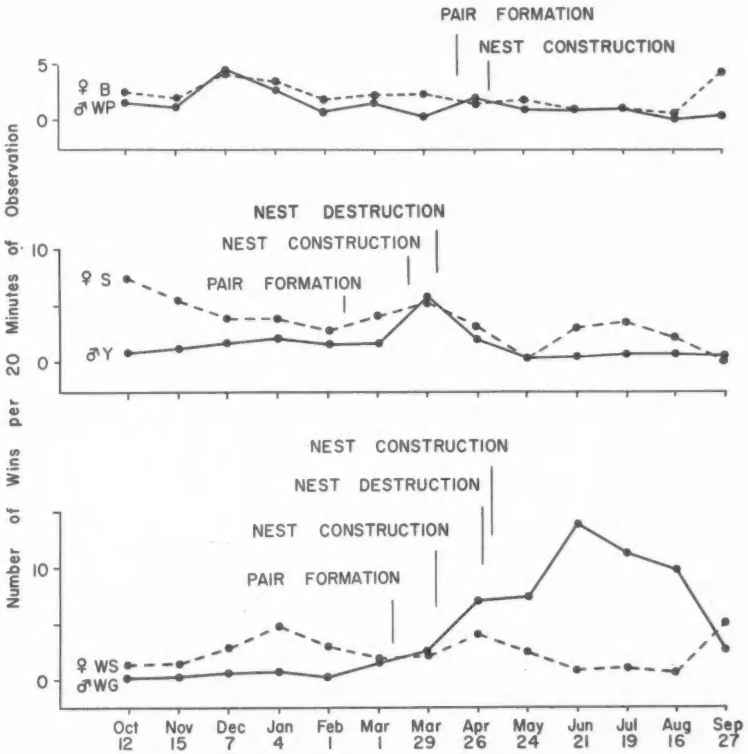

Fig. 12. Seasonal variation in the aggressiveness of three caged pairs of House Finches in 1957–58.

extreme increase in fighting behavior observed in male R, and to a lesser degree in the other males is that the entire cage becomes the territory of the male and female building a nest. The limits of the cage are well below the usual territorial limits, and hence the owners of the territory are continually being stimulated to chase away "intruders." In the wild state such territorial defense is mild, but when the intruders are unable to leave the area, the hostility increases markedly. The variable nature of this defense "drive" is shown by the highly variable degree to which a male chases his cage mates. Periods of resting and preening alternate with periods of feeding and violent supplanting attacks and chases. The male usually accompanies his mate wherever she goes, and

when she becomes active, his aggressive behavior increases. After a series of violent attacks, the male and his mate usually perch quietly side by side, preening, or just resting, for the most part ignoring the other birds in the cage.

Several caged pairs attempted to nest at the same time as another, more aggressive pair. These were never successful, but their efforts to take over the nest already being used, or to build near the same site, always increased the amount of fighting. Notice the succession of peaks of hostile behavior of individual males and females in 1957–58 (fig. 13). No two birds of the same sex reach their peak of aggressiveness at the same time. Figure 12 illustrates in a different way the same range of variation which is shown by the vertical lines in figure 7.

There is, nonetheless, much individual variation in male fighting, and it is not clear why some peaks occur where they do. The maximum in June of male WG, for example, is not correlated with any nesting activity, because his mate was not sexually active at the time; his hostile behavior rose above its level during nesting.

Figure 10 shows a decline in female group hostility at the same time that male group hostility is increasing. The decrease may be seen in the behavior of the individual females (fig. 13), as well as in the group as a whole. Despite this downward trend from the winter state, there is usually an increase of aggressiveness during nest construction and incubation. This, too, is in agreement with the behavior of wild birds, because much of the early territorial defense is initiated, if not taken over completely, by the female. Wild, incubating females have little occasion to show hostile behavior, isolated as they are, but captive females show extreme aggressive behavior when off the nest. The two females which incubated in captivity did not usually move from the nest even if other birds came up to the rim of it. In one instance a pair attempted to build a nest within four inches of the one occupied by female WR and were not often bothered by her. When the captive incubating females were off the nest to eat or drink, however, they were often belligerent toward other birds of either sex.

DEVELOPMENT OF AGGRESSIVE BEHAVIOR IN YOUNG BIRDS

Three House Finches reared by hand showed no signs of hostility toward each other until four weeks after hatching. Before this they had pecked at food particles on the feathers or beak of their companions, but the one pecked did not seem to recognize any hostile intent, and the pecking appeared to be primarily a matter of curiosity or feeding on the part of the bird which pecked. The first aggressive encounter seen was a vigorous peck by one of the males, P, at the female, O. Within a day or so, W, the other male, also began to peck at O, and within a week he pecked both O and P vigorously, chasing them from perch to perch. The pecks and supplanting attacks were accompanied by the same *chip* which is characteristic of adult quarrelling.

On June 8, ten days after the first aggressive encounter, female O began to peck both males. She was less aggressive than male W but pecked at either of her companions which perched near her. She was particularly hostile toward W.

On June 18 the young House Finches, seven weeks old, were released in the house in the company of an adult male canary. Male W performed a high intensity head-forward display, including the raising and extension of first both wings, then only one.

Wild adult House Finches often retreat from an approaching juvenile. Juveniles just out of the nest show a marked tendency to fly directly toward an object, landing on top of it instead of perching beside it. The hand-reared nestlings demonstrated this behavior and one would frequently knock another off a perch by flying directly at it and landing on top of it. When they first begin to fly, the young birds do not brake well

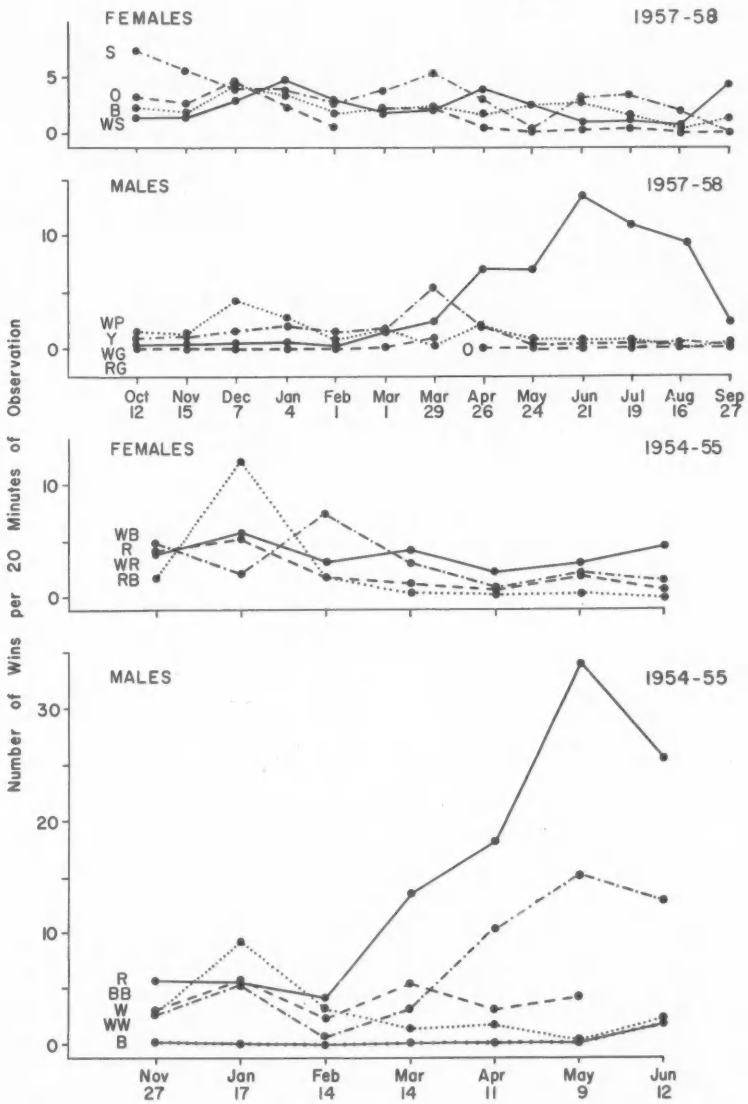

Fig. 13. Seasonal variation in the aggressiveness of individual caged male and female House Finches in 1954–55 and 1957–58.

when landing and tend to overshoot the perch. This forward momentum contributes to pushing the companion off the perch, since its hold is not very tight at this stage in development. Fledglings just out of the nest show this same tendency to fly directly toward the adults to beg for food. Usually the adult will hop to one side to avoid being hit. Since the juveniles have the same plumage pattern as the female, the adult male may mistake the oncoming bird for an adult female, and since, as will be mentioned

Table 4

Developing Behavior Patterns in Three Juvenal House Finches

Days after hatching on which new behavior was recorded	Behavior
0	Hatched
9	Taken from nest; preening, gaping, begging responses developed
12	W sleeps with head under scapular tract, whose feathers are out of sheaths
13	W and O fly well, P not well; all flap and flutter wings vigorously from time to time
15	Wing fluttering just developed to accompany begging
16	W drinks water; all three peck at seed on floor of cage
17	Birds very restless at dusk, then settle on perches to sleep
18	Begin feeding themselves to some extent; still beg
20	Birds near full size; rectrices almost full length
21	Flight still erratic
29	P singing—monotone of rapidly repeated notes
32	First bathing from rim of water dish; P pecked O, causing her to retreat
39	W pecks P, P pecks O
41	O pecks P, P pecks W
43	O pecks W, W pecks P
51	W gives complete, high intensity head-forward display to canary
54	W singing loudly—adult song posture; song more rambling and disconnected than that of adult wild male

later, males usually retreat from attacking females, he may avoid what appears to be a female attacker. The impression of attack may be heightened by the lack of fear which the juveniles display. On the other hand the behavior of the adult male may be only an attempt to dodge the approaching fledgling, learned from experience with birds just out of the nest.

Table 4 lists developing behavior patterns in three juvenal House Finches.

SOCIAL HIERARCHY

There is a well defined social hierarchy, or peck order, in flocks of House Finches. It is particularly noticeable in small groups of caged individuals. The hierarchy is fairly stable, but changes do occur from time to time. In the social hierarchy, a bird is said to be "dominant" if it can be expected to win in hostile encounters with another "subordinate" individual. The dominance described here is of the peck-right type, but occasional reverses may occur under exceptional conditions. A bird is said to win an encounter if it causes its opponent to retreat. Such hostile encounters involve the various forms of aggressive behavior already described here and in Part I.

Peck order in caged groups.—In caged groups of House Finches in winter, females are generally dominant to males. Figure 14 shows the heterosexual aggressiveness of both sexes throughout the year by indicating the number of wins of either sex over the other for every 20 minutes of observation. A comparison of the two graphs in figure 14 reveals that the patterns of male and female dominance throughout the year are not identical in 1955 and 1958, but that the general, overall patterns are about the same.

During the breeding season the females as a group are no longer dominant to the males as a group, but each mated female remains dominant to her mate. This is unlike the conditions described by Hinde (1955–1956) for some other passerine species in which the female is dominant to her mate during the breeding season, but the male is dominant to the female in the winter. It is not likely that the birds are behaving sexually throughout the year, since the gonads of both sexes regress during the winter months. Other

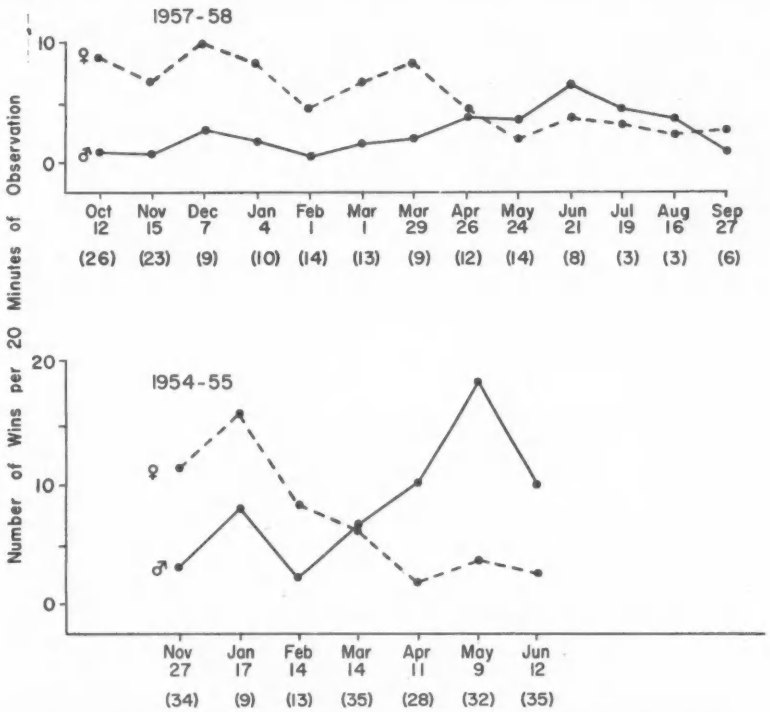

Fig. 14. Heterosexual aggressiveness of caged male and female House Finches in 1954–55 and 1957–58. Numbers in parentheses indicate the number of 20-minute observation sessions per four-week period.

manifestations of sexual activity such as male courtship display, courtship feeding, and full song do not occur in the winter, at least in caged birds. Also, a hand-reared, immature female was found to be dominant to immature males during the first winter.

There must be something other than a hold-over of sexual motivation responsible for this female dominance in winter. The dominance pattern in House Finches, therefore, is different from that of most other passerine species which have been studied, although a somewhat similar situation has been described for the Bullfinch, *Pyrrhula pyrrhula* (Hinde, 1955–1956; Nicolai, 1956). The detailed differences in dominance of males and females in 1955 and 1958 are probably related to the same factors which

were discussed previously with regard to the differences in the incidence of total aggressiveness in the two years.

The dominance of females as a group over males as a group may be observed in the hierarchies shown in table 5. The first two sections represent the hierarchies during December, 1954, and December, 1957. These show that some of the males are dominant to individual females, but in general the females are dominant as a group. One group

Table 5

Social Hierarchies of Mixed Groups of Caged Male and Female House Finches in Winter

Read from left to right in the horizontal rows. The numbers indicate the number of wins by the bird in question. For example, in the first hierarchy, RB won 7 observed aggressive encounters with WB.

November 14 to December 17, 1954

		RB	WB	R♀	WR	R♂	W	WW	BB	B
RB	♀		7	14	12	2	1	9	6	6
WB	♀			19	39	20	0	34	23	34
R♀	♀				28	28	23	23	21	18
WR	♀		1			42	2	47	1	39
R♂	♂	16	1	1	1		24	62	26	62
W	♂		29		20			21	15	16
WW	♂			1			2		26	60
BB	♂		1	2	33	1	1	2		60
B	♂			1			6			

November 24 to December 21, 1957

		S	O	B	WS	Y	WP	WG	RG
S	♀		8	4	5	8	5	3	3
O	♀			15	5	9	7	4	2
B	♀				15	16	0	3	4
WS	♀					9	10	3	4
Y	♂						11	3	2
WP	♂			25				7	7
WG	♂								5
RG	♂								

January 3 to January 31, 1959

Group A

		I	L	LW	RN	RB	SO	G	SR
I	♀		7	10	7	4	6	3	7
L	♀			3	0	3	4	3	1
LW	♀				4	0	1	4	2
RN	♀					0	1	5	10
RB	♂				1		0	2	1
SO	♂		1	2	1			1	5
G	♂								1
SR	♂				1				

Group B

		WS	B	S	PG	R	SG	GS	W
WS	♀		10	1	4	12	3	5	3
B	♀			1	2	11	2	4	2
S	♀				0	3	1	1	0
PG	♀					6	2	2	2
R	♂						6	2	3
SG	♂							2	7
GS	♂								6
W	♂								

Group C

		R	L	GB	WG	GR	WP	Y	O
R	♀		1	2	0	4	2	3	2
L	♀			2	1	2	1	1	1
GB	♀				7	7	4	6	10
WG	♀	2				6	8	8	5
GR	♀				1		3	2	5
WP	♂							8	1
Y	♂								3
O	♂						9		

of four pairs of House Finches was continued almost intact for over a year in order to observe dominance changes. At the end of the year, instead of returning to the typical winter pattern of females winning over males, a somewhat jumbled social structure was maintained. For the most part it represented the same social hierarchy as during the breeding season. It would appear, in this case, that once the birds learned a hierarchy they tended to continue it even in the absence of the stimuli which helped establish it in the first place. This same sort of phenomenon has been described in hens by Allee (1942). In January, 1959, in order to test this interpretation, three groups of House

Finches were mixed, the males of one group joining the females of another, and all were placed in cages which were unfamiliar to them. The results are shown in table 5. In all three groups females were dominant over males, and in only one was a male (WG) dominant over females (R and GR) in the beginning. Within a few weeks several males had begun to win encounters with females, but in all cages the females as a group remained dominant over the males as a group.

Comparisons with wild birds.—In contrast to the dominance of females in caged birds, encounters between wild birds, at a feeding station from September through January, were won by males more often than by females. Of 84 hostile encounters between males and females, males won 50 and females 34. Seven females and eight males were involved as winners in these 84 encounters. In the wild there appears to be no marked dominance of one sex over the other, such as is indicated by data obtained from

Table 6

Dominance Within Pairs of House Finches

Pair ♂	Pair ♀	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
R	WR	♀/♂	♀/♂	♀/♂	♀/♂	♂/♀	♀/♂	♀/♂
WW	WB	♀/♂	♀/♂	♀/♂	♀/♂	♂/♀	♂/♀	♀/♂
BB	R	♀/♂	♀/♂	♂/♀	♂/♀	♂/♀	♂/♀	.....
Y	S	♀/♂	♀/♂	♀/♂	♀/♂	♀/♂	♀/♂	♀/♂
WG	WS	♀/♂	♀/♂	♂/♀	♂/♀	♀/♂	♀/♂	♀/♂
WP	B	♂/♀	♂/♀	♂/♀	♀/♂	♀/♂	♀/♂	♀/♂

captive individuals. Males made 6.3 attacks per bird as opposed to 4.9 attacks per bird made by females during observations at a feeding station. The reason for this difference in behavior of wild and captive birds is not apparent. The behavior of the wild birds is more like that of other passerines described by Hinde (1955–1956), but it still differs somewhat because of the frequent wins by females. It would be just as unwarranted to assert that males as a rule are dominant to females in wild winter flocks as to state the reverse.

Table 7 illustrates the social hierarchies of the 1955 and 1958 caged flocks during the breeding season. There is no clear-cut dominance of one sex over the other. The members of one pair usually occupied about the same level in a hierarchy, with the female usually dominant to the male. Unmated birds fell to the bottom of the hierarchy.

It is possible that in a fairly stable, resident population, members of the population recognize each other and maintain a fairly constant hierarchy throughout the year, carrying over into the winter months, at least in part, the same rank they had during the breeding season, much as was the case in the caged birds. This explanation seems unlikely, however, since the amount of population mixture and turnover, as indicated by banding records, appears to be great. Only a small proportion of the House Finches which are banded during the year at a given place are seen there again. It is true that a core of resident birds does remain throughout the year, and many of these were involved in the encounters observed, but of 31 pairs involved in such recorded encounters, only 12 were recorded more than once. The largest number of encounters recorded for a given pair is four (for three pairs), and in every instance these were recorded in a single day. In only one pair were the members seen to fight each other on more than one day. Several of the birds involved in encounters in January had been banded as juveniles in the previous year and so could not have been a part of the breeding hierarchy at that time. Previous experience in a breeding population hierarchy does

not appear to be a plausible explanation for this lack of conclusive female dominance in the wild population.

Dominance within pairs and within a given sex.—In five out of six caged pairs observed the male dominated his mate for a brief period just before pair formation (see table 6). The reason for this is apparently that the male was initiating pair formation by the billing performance. The female is less resistant to the male's advances than at other times of the year and allows him to approach closely to bill. She usually avoids the male if she is not receptive instead of supplanting him directly, as would be the normal procedure outside the breeding season. The actual basis for the change in aggressive motivation is not known, but it appears to be related to changes in levels of the sex hormones.

Table 7

The Relation of Weight to Position in Social Hierarchy

Bird	Sex	Rank in hierarchy	Rank in weight	Bird	Sex	Rank in hierarchy	Rank in weight
RL	♂	1	2	R	♂	1	2
SB	♂	2	3	WW	♂	2	1
BW	♂	3	4	W	♂	3	4
PL	♂	4	1	B	♂	4	3
GL	♂	1	2	WR	♂	1	2
GW	♂	2	1	WB	♀	2	3
OR	♂	3	3	R	♀	3	1
BR	♂	4	4	RB	♀	4	4
OS	♂	1	4	R	♂	1	3
OP	♂	2	2	WR	♀	2	4
RL	♂	3	1	WW	♂	3	1
WO	♂	4	3	WB	♀	4	5
				R	♀	5	2
P	♂	1	1	W	♂	6	7
G	♂	2	2	B	♂	7	6
R	♂	3	4	RB	♀	8	8
SB	♂	4	3				

Male WP was dominant to female B throughout the winter. Later, she became his mate. In this case the dominance of the male lasted for a much longer time than usual.

Besides the dominant-subordinate relation of the two sexes toward each other, there is the question of the causes of dominance relations between individuals of the same sex. Factors such as breeding condition of the individual, general state of health, age, weight, the shade of red of the plumage of males, territory, and "native belligerence" or genetic background of aggression, in addition to the previous experience of the individual, all might play some role in determining position in the social hierarchy.

Breeding condition is particularly important in determining social rank during the breeding season, and it is especially noticeable in the males, which may move from near the bottom of the peck order in a cage in winter to the top of the hierarchy in the spring. Birds that come into breeding condition first and become mated rise in the hierarchy more rapidly than other males which are slower to reach full gonadal development, fail to obtain mates, or for some other reason are retarded in developing sexual behavior.

Male B in 1955 was an example. Although he was at the bottom of the social order in the fall and winter, he might have been expected to rise in the hierarchy as did the other males during the spring. Instead he remained at the bottom of the scale. In April

and May he became active in courting a female which was already mated. When her mate escaped from the cage in June, B became paired with her and immediately assumed a higher position in the hierarchy.

Male WG in 1958 serves as another example. He moved from next to last to second in the hierarchy, dominated only by his mate (WS).

Females, likewise rise in the hierarchy in the spring according to their breeding status. Female WS just mentioned rose from last place in the female hierarchy to the alpha position for the entire flock. This is not to be confused with the change of rank which Lorenz (1952) described in the Jackdaw (*Corvus monedula*), in which the one member of the pair rises at the time of pair formation to the same status as the other member. In the House Finch both members of the pair rise in the hierarchy, but they do not necessarily rise to the same level. Only male WG in 1958 rose to the level of his mate, and he remained subordinate to her, not of equivalent status. Male Y, which in 1955 came closest to equaling WG's rise in social position, out-ranked only one female, which was unmated and was added to the flock six months after it was established. Even at the time male Y chased the other males vigorously, while his mate was building a nest, he was still subordinate to three females, including his mate.

For the most part all the caged birds appeared to remain in good health. Those which showed illness usually died very shortly, before any changes in social status were evident. Schjelderup-Ebbe (1935) states that the usual outcome of fights between healthy and unhealthy individuals is success for the healthy one. Allee (1942) has suggested that fatigue or illness at the time of some initial encounters may produce the triangles which occur so frequently in diagrams of social hierarchies. One member of the 1955 flock, female RB, had only one leg when captured. She was thereby at a disadvantage, but she won most of her initial encounters when placed with the other birds in the cage. Gradually, however, she lost her alpha position and sank to the bottom of the hierarchy, remaining dominant only to male B. She had lost many feathers so that bare spots of skin were visible on her head. She perched with difficulty because of the one leg and moved about only with great exertion. Probably she lost her original status because of her inability to move about as easily as the other birds and to attack others as readily as they attacked her. Probably, also, she became fatigued more quickly than her opponents. When male B finally found a mate, he, too, overcame RB and she remained in the omega position from then on. Allee (1942) suggests that other members of the flock are quick to recognize signs of weakness on the part of a superior and to take advantage of the weakness to overcome the opponent.

Age or maturity is sometimes considered a possible factor concerned with social status. Since all the birds studied in the caged flocks were adult when captured, this factor could be ruled out for the caged flock. Encounters between adults and juveniles have been observed in the wild, however, and juveniles have often won over adults. Absolute age seems to be of little or no importance in adult hierarchies, since few, if any, birds live to become old and feeble.

Weight or size would appear to be a likely factor in determining success in initial encounters. Table 7 presents the weights of all birds in the 1955 flock and those of all males in the 1958 groups. The correlation coefficient of weight and social status for all groups, obtained by using a measure for degree of relationship of ranks ($P=1-\frac{6(\Sigma D^2)}{N(N^2-1)}$), was 0.38, a very low degree of correlation. Collias (1943) using a different method obtained a correlation coefficient of $0.47\pm.073$ between weight and social rank in hens.

By using the measure for relationship of ranks, the correlation of the shade or

intensity of red in the male plumage with rank in the male hierarchy was determined (table 8). Again a low correlation coefficient of 0.2 was obtained. The relative unimportance of color may be shown more strikingly perhaps by noting that the first male to obtain a mate and to become the alpha male was a pale yellow color, whereas two of his companions had bright red plumage on head, breast, and rump. Also, male B in 1955, the omega male, was second in intensity of color. Color, then, seems to be of small importance, if indeed it plays any role, in determining social status.

Familiarity with the area has been shown by Schjelderup-Ebbe (1922, 1935) and others to be of great importance in determining which one of two birds will dominate the other. This has been borne out to some extent in the present study but not to the

Table 8

The Relation of Plumage Color of Males to Position in Social Hierarchy

Bird	Rank in hierarchy	Rank in color
R	1	1
WW	2	3
BB	3	4
W	4	2
WP	1	2
Y	2	3
WG	3	1
RG	4	4
P	1	3
G	2	4
R	3	1
SB	4	2

degree which might be expected. Individuals which were introduced into the caged flocks after others in the flock were well established usually assumed a position near the bottom of the social hierarchy among members of their own sex. For example, female PG was added to one caged flock six months after it was first established. She assumed a position second from the end of the female hierarchy, but she was dominant to all the males except WG. Male X was introduced seven months after the establishment of the flock, and he assumed second place in the male hierarchy, dominated by all females. Male O was introduced one month later and took the omega position in the hierarchy. Several factors probably contributed to this in addition to unfamiliarity with the new surroundings. By this time the other three males were mated and probably partly because of this, they dominated the unmated male O. In addition, first male Y and then male WG patrolled the cage chasing other males vigorously, and singling out O as the particular object of their aggression. Probably fatigue from the almost continual chasing and supplanting by the dominant males, as well as the unfamiliar surroundings, and the lack of the boost of aggression which pair formation seems to provide contributed to the maintenance of O in the omega position.

When 11 males were placed in one cage, in which four of them had been previously, three of these four won encounters with all the strangers. The fourth lost to only two of the new individuals. This bears out quite well the accepted idea of the importance of familiarity with surroundings in determining the outcome of aggressive encounters between individuals. A week later the more aggressive, introduced individuals were beginning to climb in the peck order.

Somewhat related to this familiarity with an area is the matter of territoriality or

the ownership and defense of an area. The caged House Finches observed in this study did not establish separate territories within the cage, as Shoemaker (1939) recorded for his canaries and Bennett (1939, 1940) and others for pigeons. Instead, the alpha pair acted as if the entire cage were their territory. The beta pair was prevented by the alpha pair from breeding. They displayed a strong inclination to nest, however, inspecting nest sites, particularly the nest of the alpha pair, and chasing birds subordinate to them in the hierarchy. They, too, showed signs of territoriality but to a much smaller degree than the alpha pair. The gamma pair showed very weak tendencies toward nesting, and they were much less aggressive than either the alpha or beta pair. The three pairs may be thought of as holding a single territory in common but defending it with varying degrees of aggressiveness. The alpha pair was the primary territory holder, the beta pair the secondary holder, and the gamma pair the tertiary holder. The two unmated birds were attacked by all others in the cage and may be thought of as intruders in the territory of each of the other pairs.

Writing about the peck order of canaries, Allee (1942:143) stated that "when they are confined in a small space, the social order becomes relatively simple and definite; it is little complicated by territoriality. Given more space, individual territories tend to become established in which the territory holder is usually supreme. . . . Even a socially low-ranking male normally dominates other males in some restricted space about his nest." In the case of the House Finches just described the effect is of a reduction of the available area until the territories of several pairs become contiguous.

Territorial behavior is characteristic of the breeding season when the different pairs are attempting to nest and their success in building a nest is dependent on their success in establishing a territory, but its relation to the dominance behavior observed in winter when there are no territories and the birds are in flocks is not clear.

Finally, there is the matter of "native belligerence," or the genetic background of the aggressive behavior of any individual. Potter (1949) demonstrated that hens of different breeds vary in their aggressiveness. Hens of some breeds consistently win in encounters and hens of other breeds just as consistently lose. Furthermore, this tendency to win is not necessarily related to weight or breeding condition (Ginsburg and Allee, 1942). Scott (1958) discussed the difference in aggressiveness of various strains of dogs. Leopold (1944) described a hereditary wildness factor in turkeys. In House Finches and in other animals, however, it is very difficult to separate the inherited from the learned behavior. Undoubtedly much of the difference in individual aggressive behavior is due to previous experience. The whole spectrum of motivational influences from physiological to learned factors is involved. But, as Scott and also Ginsburg and Allee suggest, apart from anatomical and physiological factors there is probably also some genetic control of the threshold of aggressive reactions to various situations and stimuli. It is true that the genetic differences described for dogs and hens are between distinct strains which do not usually interbreed and that such wide divergence would not be expected in a freely interbreeding population. Individual differences would be expected to occur in a panmictic population, however, and some would be almost if not just as great as those between separate breeds of hens. But there should be many more intermediate conditions between the two extremes. Variation in intensity of territory defense by different individuals of a given species may be observed in the field, and it is not impossible, or even improbable, that part of this variation has a genetic basis.

Interspecific relations.—At feeding places and on perches House Finches sometimes supplant other species and are sometimes themselves supplanted by other species. Species to which House Finches may be said to be dominant and species to which they are usually subordinate are listed here.

Species attacked by House Finches	Species which attack House Finches
Contopus sordidulus	*Contopus sordidulus*
Passer domesticus	*Passer domesticus*
Spinus psaltria	*Pipilo fuscus*
Serinus canarius	*Melospiza melodia*
Junco oreganus	*Chamaea fasciata*
Zonotrichia leucophrys	

Usually a House Finch merely supplants an opponent of a different species, but occasionally head-forward displays may be performed in instances of strong conflict, as between House Finches and House Sparrows (*Passer domesticus*) at a feeding station. Hand-reared House Finches performed the extreme form of the head-forward display toward a canary.

DISCUSSION

Although hostile behavior occurs more frequently among groups of caged House Finches than among free-living ones, the same postures and call notes are employed in both situations. The significance of some aggressive patterns is not clear, however, until they have been studied under natural conditions. On the other hand, some behavior patterns become more understandable when observed more closely in captivity. The combination of field and laboratory study has proved to be almost essential in the description and interpretation of House Finch behavior.

The dominance pattern of the House Finch differs from that of the canary, Greenfinch (*Chloris chloris*), Continental Goldfinch (*Carduelis carduelis*), Hawfinch (*Coccothraustes coccothraustes*), Chaffinch (*Fringilla coelebs*), and Brambling (*Fringilla montifringilla*), as the males are not generally dominant to the females in winter. Captive female Bullfinches have been reported (Hinde, 1955–1956) to be on the whole dominant to the males in winter, and this resembles more the condition in the House Finch. The female of a pair of House Finches, however, remains dominant to her mate during the breeding season. In this respect, the House Finch resembles the species studied by Hinde. He reports that some male canaries may continue to make occasional attacks up to the time of copulation. A similar situation was observed in one pair of House Finches. These birds were confined in a very small (18 × 18 × 12 inch) cage, however, and the lack of space might have elicited abnormal behavior. Other wild and caged males were not seen to attack their mate after the pair bond was established. In general, the seasonal variation in dominance of male and female House Finches seems to agree most closely with that of Bullfinches.

Noble, Wurm, and Schmidt (1938) found that the male Black-crowned Night Heron (*Nycticorax nycticorax*) is dominant to the female during the breeding season, and they postulated that this male dominance was necessary if copulation was to be successful. Such a condition is not necessary for successful mating in many passerine birds, in which the dominance of the sexes is reversed from the pattern in night herons. Table 9 lists species in which the female is dominant.

In the House Finch, copulation usually occurs at the invitation of the female. In most other species the female may be stimulated to solicit by a male display or may solicit without male display. In either case actual copulation, when successful, is usually initiated by the female with no overt signs that the male is necessarily dominant immediately before the act.

Tinbergen (1939), Nice (1941), and Lack (1943) interpret the function of male bird song as a warning toward rival males or as a means of attracting females, or both.

Moynihan and Hall (1954) suggest that the term "song" be limited to vocalizations which serve both functions. This definition is followed by Smith (1959). Morris (1958), however, suggests that the earlier interpretation of song, as having either function or both, be recognized, and it is this definition which is used here. Although male song may sometimes lead to hostile encounters between male House Finches, this is of relatively rare occurrence, and it seems incorrect to imply that this is one of the major functions of House Finch song. The primary function appears to be the attraction of a female, because unmated males, or a male whose mate is incubating sings much more frequently and more vigorously than males in the company of their mates. It is quite

Table 9

Male and Female Dominance in Breeding Season, Especially during Copulation

Male dominant	
Pygoscelis papua	Roberts, 1940
Gallus domesticus	Masure and Allee, 1934*a*
Melopsittacus undulatus	Masure and Allee, 1934*b*
Nycticorax nycticorax	Noble and Wurm, 1940
Anas platyrhynchos	Allee, 1942
Larus atricilla	Noble and Wurm, 1943
Columba livia	Allee, 1942
Streptopelia risoria	Bennett, 1940
Plectrophenax nivalis	Tinbergen, 1939
Female dominant	
Chloris chloris	Hinde, 1955–56
Coccothraustes coccothraustes	Hinde, 1955–56
Fringilla coelebs	Hinde, 1955–56; Marler, 1956
Fringilla montifringilla	Hinde, 1955–56
Carduelis carduelis	Hinde, 1955–56
Serinus canarius	Hinde, 1955–56

possible, however, that loud singing by males may lead to some dispersal of individual males, because two singing males usually perch farther apart than when they are not singing. Probably, therefore, there is an aggressive element in vigorous singing by male House Finches, but it is never so apparent as in the song duels of the Snow Bunting (*Plectrophenax nivalis*) or Song Sparrow (*Melospiza melodia*).

Many of the fringillids which were studied by Hinde (1955–1956) perform a display somewhat similar to the display of male House Finches. The non-aggressive, sleeked, wings-raised posture which Hinde describes for the male canary resembles the House Finch display somewhat, but it is given under different circumstances, apparently involves a much stronger tendency to attack, and it may be performed rarely by the female. The sleeked, wings-raised display of the male Greenfinch (Hinde, 1955) and sleeked, horizontal posture of the male Hawfinch (Hinde, 1955–1956) likewise appear to involve a stronger aggressive motivation than the House Finch display, but they resemble it more closely than does that of the canary because the Greenfinch and Hawfinch displays, like the House Finch display, sometimes involve pivoting. Pivoting is a very conspicuous part of the displays of the Continental Goldfinch, but it is not combined with the wings-drooped posture which seems to correspond to the non-aggressive wings-raised posture of the canary and the display of the male House Finch. The dance of the male Bullfinch is reminiscent of the House Finch display, particularly in the

circumstances in which it occurs, but the posture involved does not correspond very closely to that assumed by the House Finch. Similarly the lopsided, wings-drooped posture of the Chaffinch (Hinde, 1955, 1955–1956; Marler, 1956) has only a slight resemblance to the House Finch display. Of all these species only the Greenfinch and House Finch sing while performing the display, although the Continental Goldfinch may utter call notes, and the Bullfinch is said to give a coarse low warble. Horizontal pivoting and song are characteristic elements of some estrildine, pre-copulatory displays, but the postures of the birds generally are not like the House Finch display posture (Morris, 1958). It is of interest, although not necessarily significant, that the "courtship" posture most like that of the House Finch is the display posture of the male House Sparrow, a ploceid (Daanje, 1941; Summers-Smith, 1954).

In general the agonistic postures and behavior of House Finches closely resemble those of other fringillids (Hinde, 1955–1956). As Hinde remarks, these behavior patterns appear to be very widespread among all the passerines. Nevertheless, House Finch behavior suggests some alternate interpretations to those given by Hinde (*op. cit.*) and Marler (1956). According to their interpretation a horizontal body position as in head-forward display or fright is associated with a tendency to flee. As was noted previously, display is supposedly associated with conflicting motivation, and it might be assumed that a conflict between a tendency to attack and a tendency to flee would result in a head-forward display. As Hinde mentions, however, the bird with the more horizontal posture is the more likely to attack. This does not appear to be consistent with the idea that the horizontal posture is associated with a tendency to flee, since the bird with the more horizontal posture would be expected to be the one to flee, whereas in fact it is usually this bird which attacks. If on the other hand we think of the situation only in terms of conflicting motivation—both escape and attack tendencies strong and of about equal strength—then the bird with the more horizontal posture, that is, the one with the greater conflict, should not consistently attack or flee, but the outcome should be random, depending on which tendency is stronger. Because neither explanation seems to fit the observed behavior exactly, it is much simpler to think of the horizontal posture of either an aggressive head-forward display or of a fright reaction as merely an intention to fly. In either case—attacking or fleeing—the bird flies. Since in a head-forward display the body is pointed toward another bird, whereas in the fright reaction the body usually points away from other individuals toward a clear flight space, the birds should have no difficulty in distinguishing the two intentions. The different circumstances in which the two displays occur, the utterance of a loud call note with a head-forward display, and the silent crouch of the fright reaction, at least in the House Finch, must also make the meaning of the posture clear to other birds. Thus the two almost identical postures retain their separate signal function because of the different contexts in which they are given.

The fluffing of body feathers of subordinate individuals during conflicts with more aggressive birds has not been observed in the House Finch. Only feathers of the forehead may be slightly erected when a bird appears mildly afraid. Aside from fluffing by birds when resting, preening, sleeping, or when sick, fluffing occurs only in some head-forward displays. There is no direct evidence, then, that in the House Finch fluffing is associated with thwarted fleeing or that it serves as a submissive posture as Hinde suggests to be the case in the eight species he studied. It is possible, of course, that the fluffing which sometimes occurs during a head-forward display may result from a fleeing tendency which is blocked or overbalanced by an attack tendency. Or, this fluffing may be a ritualized pattern which has been carried over from the agonistic context in which it occurs in some other fringillids. More observation is needed to clarify this point.

The lack of a well-defined and stoutly defended territory beyond the immediate vicinity of the nest or the mate is probably associated with the close spacing of nests, although it is not possible to say which is cause and which is effect. The very mild aggressive element in male song is undoubtedly connected with the limited territoriality of the species. The lack of a conspicuous, pre-copulatory display, or the displacement of a phylogenetically earlier display of this sort into a different context such as seems to have occurred in the House Finch and House Sparrow, is probably tied in with the small size of territories and the continual proximity of nesting pairs. The importance of isolation for the success of coition has been pointed out earlier. It should be mentioned, however, that the need for isolation breaks down as the proximity of nests increases and a colony is formed. Colonial species do not require privacy for the successful performance of the sex act. The sight of copulation is not so stimulating to onlooking males that they attempt to interfere. The House Sparrow, a semicolonial species which nests in denser groupings than the House Finch, has reached this stage, but the House Finch has not.

The so-called "Darling effect," or the synchrony of the breeding activities of a colony, places a premium on mutual stimulation by members of a group (Darling, 1938). It is perhaps significant that three species which nest in loose groupings, the House Finch, Greenfinch, and House Sparrow, have a conspicuous display performance involving a "dance" and loud song. In at least two of these, the House Finch and the House Sparrow, the display may involve several males at one time. These communal displays may serve the same sort of function as the displays of members of a colony of sea birds in bringing about a close synchrony of breeding activity among the members of the group and in stimulating more birds to breed.

It is important to relate the display repertoire of any species to its ecology, insofar as this is possible. Most ethologists and ecologists would agree that the way of life of any successful species, including its various behavior patterns, is closely bound by selective forces to the environment in which it lives. There has been mention of several behavior patterns of the House Finch which can be tied to the semicolonial nesting of the species. What is there, then, about the ecology of the House Finch that causes it to form large flocks or feeding aggregations and to nest in loose clusters?

Nests are too widely spaced for the aggregations to be considered colonies, and the proximity of nests is undoubtedly due at least in part to the localization of optimal nesting sites. The territory of a pair of House Finches includes only a small area around the nest and does not include a foraging space. Other species such as the Song Sparrow include a foraging area inside the strongly defended territory limits. Most territorial species utilize a great variety of food items and are thus able to live within a small area. But House Finches feed exclusively on seeds and fruits and, unlike most other passerines, do not take insect food. They utilize only a small portion of the total available food types and have become adapted to moving from place to place to locate the proper items. Characteristically, large numbers of finches may be seen feeding in open fields where weed seeds or fruits are abundant. As soon as this food source is exhausted the birds move on to other, more rewarding sites. House Finches and other American members of the genus *Carpodacus* are commonly observed to fly long distances between feeding and nesting areas. A similar separation of defended nesting territory and neutral feeding area is described for the Scarlet Grosbeak (*Carpodacus erythrinus*) by Haas (1939). Bates and Lowther (1952) suggest a semicolonial nesting habit in the Scarlet Grosbeak much the same as is often found in the House Finch. Possibly the same factors of specialization in feeding and localization of optimal nest sites are involved in both species.

SUMMARY

This part of a study of the agonistic behavior of the House Finch is concerned with factors in aggressiveness and in sociality and with the possible significance of certain behavior patterns in free-living populations. (See Thompson, 1960:269, for a summary of Part I.)

Experiments with caged birds indicate that the incidence of aggressive behavior increases when the amount of space available to each bird is strongly decreased.

Observations of caged birds indicate that peaks of aggressive behavior occur in late fall, early spring, and late June. The cause of the peaks and the intervening troughs is not clear, but several factors are suggested. The increase in total aggressiveness of the group during the breeding season is due to an increase in the aggressiveness of a few individuals rather than of the group as a whole. Males were found to be more aggressive than females in the spring. This rise of male aggressiveness is undoubtedly related to the defense of mate and territory.

There is a well-defined social hierarchy in captive flocks of House Finches. Caged females generally are dominant to males in the winter. During the breeding season the females as a group are no longer dominant to the males as a group, but each mated female remains dominant to her mate. In contrast to the dominance pattern of caged birds, encounters between wild birds at a feeding station between September and January were won by males more often than by females. There is no clear pattern of one sex as a group being dominant to the other. The reasons for this discrepancy in wild and captive flocks are not apparent.

At feeding places and on perches House Finches sometimes supplant other species, and they in turn are sometimes supplanted by other species. Circumstances determining which species will win an encounter vary.

Factors which seem to have bearing on the position of an individual in the social hierarchy are breeding condition, general state of health, familiarity with the area, territory, native belligerence, and previous experience.

It is suggested that the horizontal posture of either a head-forward display or a fright reaction may be interpreted as merely an intention to fly rather than an indication of a tendency to flee.

Although the primary function of male song during the breeding season appears to be advertisement for a mate, song does seem to involve weak aggressive motivation, and it may lead to some dispersal of individual males.

The lack of a well-defined and stoutly defended territory beyond the immediate vicinity of the nest or the mate, the very mild aggressive element in male song, and the lack of a conspicuous, pre-copulatory display, or the displacement of an earlier display of this sort into a different context, may be related to the semicolonial nesting habits of the species.

LITERATURE CITED

Allee, W.C.

1942. Social dominance and subordination among vertebrates. Biol. Symp., 8:139–162.

Bates, R. S. P., and Lowther, E. H. N.

1952. Breeding birds of Kashmir (Oxford Univ. Press).

Bennett, M. A.

1939. The social hierarchy in ring doves. Ecology, 20:337–357.

1940. The social hierarchy in ring doves. II. The effect of treatment with testosterone propionate. Ecology, 21:148–165.

Collias, N. E.

1943. Statistical analysis of factors which make for success in initial encounters between hens. Amer. Nat., 77:519–538.

Daanje, A.
1941. Über das Verhalten des Haussperlings (*Passer d. domesticus* L.). Ardea, 30:1–42.
Darling, F. F.
1938. Bird flocks and the breeding cycle: a contribution to the study of avian sociality (At the University Press, Cambridge [England]).
Ginsburg, B., and Allee, W. C.
1942. Some effects of conditioning on social dominance and subordination in inbred strains of mice. Physiol. Zool., 15:485–506.
Haas, G.
1939. Beiträge zum Vorkommen und sur Fortpflanzungsbiologie des Karmingimpels am Drausensee. Beitr. Fortpflbiol. Vögel. Berlin, 15:52–62.
Hinde, R. A.
1955. The courtship and copulation of the greenfinch (*Chloris chloris*). Behaviour, 7:207–232.
1955–1956. A comparative study of the courtship of certain finches (Fringillidae). Ibis, 97: 706–745; 98:1–23.
Lack, D.
1943. The life of the robin (H. F. and G. Witherby, Ltd., London).
Leopold, A. S.
1944. The nature of heritable wildness in turkeys. Condor, 46:133–197.
Lorenz, K.
1952. King Solomon's ring (Thomas Y. Crowell Co., N. Y.).
Marler, P.
1956. Behaviour of the chaffinch (*Fringilla coelebs*). Behaviour Supplement No. 5:viii+1–184.
Masure, R. H., and Allee, W. C.
1934*a*. The social order in flocks of the common chicken and the pigeon. Auk, 51:306–327.
1934*b*. Flock organization of the shell-parakeet, *Melopsittacus undulatus* Shaw. Ecology, 15: 388–398.
Morris, D.
1958. The comparative ethology of grassfinches (Erythrurae) and mannikins (Amadinae). Proc. Zool. Soc. London, 131:389–439.
Moynihan, M., and Hall, M. F.
1954. Hostile, sexual, and other social behaviour patterns of the spice finch (*Lonchura punctulata*) in captivity. Behaviour, 7:33–76.
Nice, M. M.
1941. The role of territory in bird life. Amer. Midl. Nat., 26:441–487.
Nicolai, J.
1956. On the biology and ethology of the bullfinch (*Pyrrhula pyrrhula* L.). Zeit. für Tierpsych., 13:93–132.
Noble, G. K., and Wurm, M.
1940. The effect of testosterone propionate on the black-crowned night heron. Endocrinology, 26:837–850.
1943. Social behavior of the laughing gull. Ann. N. Y. Acad. Sci., 45:179–220.
Noble, G. K., Wurm, M., and Schmidt, A.
1938. Social behavior of the black-crowned night heron. Auk, 55:7–40.
Potter, J. H.
1949. Dominance relations between different breeds of domestic hens. Physiol. Zool., 22:261–280.
Roberts, B.
1940. The breeding behavior of penguins with special reference to *Pygoscelis papua* (Foster). Brit. Graham Lands Exped. 1934–37. Ser. Rept., 1:195–254.
Schjelderup-Ebbe, T.
1922. Beiträge zur Socialpsychologie des Haushuhns. Zeitschr. f. Psychol., 88:225–252.
1935. Social behavior of birds. *In* C. Murchison, Handbook of social psychology (Clark Univ. Press, Worcester, Mass.).

Scott, J. P.
1958. Aggression (Univ. Chicago Press).
Shoemaker, H. H.
1939. Social hierarchy in flocks of the canary. Auk, 56:381–406.
Smith, R. L.
1959. The songs of the grasshopper sparrow. Wilson Bull., 71:141–152.
Summers-Smith, D.
1954. The communal display of the house-sparrow *Passer domesticus*. Ibis, 96:116–128.
Thompson, W. L.
1960. Agonistic behavior in the house finch. Part I: Annual cycle and display patterns. Condor, 62:245–271.
Tinbergen, N.
1939. Field observations of East Greenland birds. II. The behavior of the snow bunting in spring. Trans. Linn. Soc. N. Y., 5:1–94.

Museum of Vertebrate Zoology, University of California, Berkeley, California, April 4, 1960. (Present address: Department of Biology, Wayne State University, Detroit, Michigan.)

FROM FIELD AND STUDY

Speed of the Allen Hummingbird While Diving.—To perform the power dive that is such a spectacular part of the display of Allen Hummingbirds (*Selasphorus sasin*), a male climbs 50 feet or more into the air and then under what appears to be full power swoops down toward the earth. The velocity during this dive must be close to maximum for the species.

Early in March of 1960, a male Allen Hummingbird displayed frequently to one or more females feeding and perching in some flowering quince bushes in Orinda, California. Next to these bushes I erected two 20-foot poles marked in 1-foot intervals and took motion pictures of the diving bird with a stationary camera fixed 33 feet from one of the poles and 40 feet from the other. The camera was aimed to record the part of the dive extending from about 25 feet above the ground down to about 15 feet. The bottom of each dive was at about 6 feet. When all went well I obtained a series of four to ten exposures of one of the poles and of the bird during that part of the dive when its speed would be expected to be greatest. The shutter opening was closed to one-quarter of the usual setting, to shorten the duration of each exposure, and the indicator on the camera was set at a speed of 64 frames per second. By photographing the face of an electric clock I found that this gave an actual speed of 69 exposures per second.

As each dive was photographed, I recorded in my notes the direction from which the bird approached one of the poles and, when the bird swooped in from one side, an estimate of how many feet from the pole it had passed. The developed strips of film were projected, exposure by exposure, in a photographic enlarger and a tracing made of the position of the bird in successive pictures. The distance between successive images of the bird was then measured, compared with the 1-foot marks on the pole in the same photograph, and corrected for being closer to or farther from the camera than the pole was. The pictures show that in the middle of its dive the bird was descending at an angle of about 45° from the horizontal. Consequently, the bird's distance from the camera was changing rapidly during all dives except those in which he approached the pole from either the right or the left; in the latter examples he provided a profile view of the arc of his dive. Using only the five dives that were recorded satisfactorily in profile and in which the bird was judged to have passed less than 4 feet from one of the poles, the speed was calculated to be 53, 53, 58, 63, and 64 miles per hour.

Some of the variation in these determinations arises from actual differences of speed in different dives, from inaccuracies in measurement of the projected images, from slight deviations from strictly profile views, and especially from errors in estimating how far away from the pole the bird passed. With the camera 33 feet from the pole and with the lens used (focal length 25 mm.), an error of 3 feet in estimating pole-to-bird distance would introduce an error of about 10 per cent in the answer.

A rough check on the accuracy of these measurements can be obtained by estimating the height of the dive and the elapsed time. The bird appeared to dive about 60 feet in slightly more than 1 second, which gives an average speed of 40 miles per hour, but this includes a period of acceleration at the beginning of the dive and a period of deceleration near the bottom.

Shortly before the bottom of many of the dives, the bird begins a long, clear, whistling note that arises from the vibration of certain tail feathers (Aldrich, Condor, 58, 1956:126). To determine the speed at this time, a few series of pictures were taken as the bird levelled off and passed over or through the top of the bush. From three such series of pictures, the speed at the bottom of the dive, as the bird moved horizontally, was calculated to be 34, 39, and 45 miles per hour.—Oliver P. Pearson, *Museum of Vertebrate Zoology, Berkeley, California, May 10, 1960.*

Thyroid Activity in Nestling Vesper Sparrows.—Although the importance of the thyroid glands to growth and development is widely appreciated, no analysis has been made of their functional state as it relates to the establishment of homeothermy in young altricial birds. It was therefore of interest to carry out a histological study of these endocrine glands in young Vesper Sparrows (*Pooecetes gramineus gramineus*) of known age, whose growth and temperature regulation have been analyzed (Dawson and Evans, Condor, 62, 1960:329–340). Height of the secretory epithelium has been used as an index of thyroid activity.

This study was supported in part by grants from the Horace H. Rackham School of Graduate

Studies of The University of Michigan, and from the National Science Foundation (G–2096). We wish to acknowledge the assistance of P. R. Elliott and T. J. Rupp.

The thyroid glands from 36 young Vesper Sparrows were removed within 12 hours of the time when the birds were captured. Prior to sacrifice these animals had been subjected to the maintenance and experimental procedures described by Dawson and Evans (*op. cit.*). Five adult Vesper Sparrows were collected on August 6, 1955, and their thyroids were used for comparative purposes.

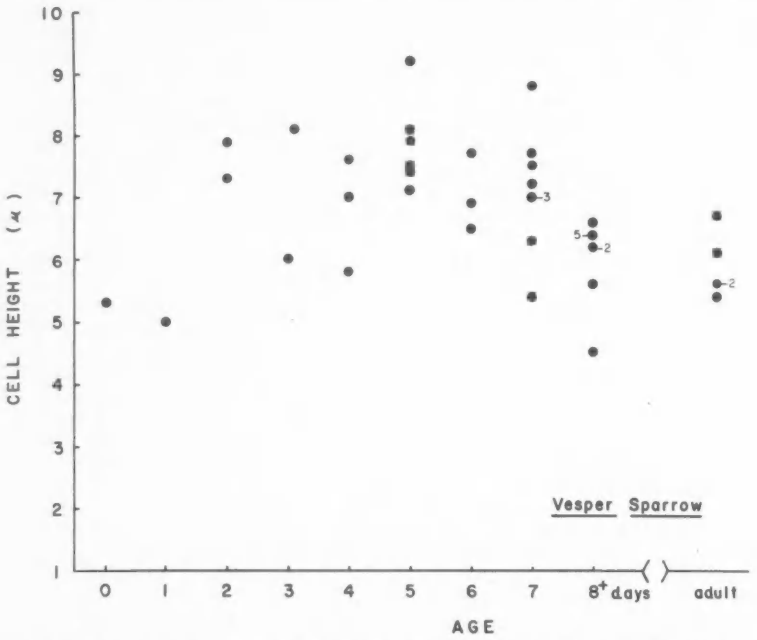

Fig. 1. Height of secretory epithelial cells in micra in the thyroids of Vesper Sparrows of various ages. The age category "8+ days" includes fledgling birds 8 to 12 days old. Numerals indicate the number of birds represented by the points which they accompany.

Thyroid tissue was fixed overnight in Bouin's solution. Ten-micra sections were cut and stained with hematoxylin. The heights of the secretory epithelial cells were determined with a compound microscope fitted with a suitably calibrated ocular micrometer. On each slide 50 fields were selected randomly. In each of these, two cells from opposite sides of a follicle were measured. Care was employed to select only round follicles to avoid possible errors arising from an oblique cutting plane. Each of the values presented in this report represents the mean for 50 pairs of observations.

The heights of thyroid secretory epithelium from Vesper Sparrows of various ages are summarized in figure 1. The data indicate thyroid activity to be at levels matching or exceeding that noted in adults throughout the nestling period. This activity appears to reach a peak on the fifth day after hatching, a day or two in advance of the time when homeothermy becomes well established in the Vesper Sparrow (Dawson and Evans, *op. cit.*). It declines at the end of the nestling period, and cell heights in fledglings 8 to 12 days old are significantly lower than those evident in nestlings 5 days old ($P<0.01$). The cell heights noted in the fledglings do not differ significantly from those noted in adult Vesper Sparrows collected in early August.

Thyroid activity of Vesper Sparrows appears highest in the period of most rapid post-hatching growth and of feather development. This activity should contribute to these processes in this species, for thyroid deficiency is known to result in plumage abnormalities and arrest of growth in young birds (Hohn, Ibis, 92, 1950:464–473). It is clear that the establishment of homeothermy in the Vesper Sparrow is not limited by the functional state of the thyroid glands. Indeed, the condition of these endocrine organs through most of the nestling period may be regarded as permissive to the development of temperature regulation, not only through the overall influence of their secretory products on growth and feather development, but also through the immediate action of these products in elevating heat production through stimulation of oxidative metabolism. The fact that thyroid activity in newly hatched Vesper Sparrows appears relatively high suggests that the anterior pituitary synthesizes and releases thyrotrophic hormone in effective amounts while the birds are still in the egg. —WILLIAM R. DAWSON and JOHN M. ALLEN, *Department of Zoology, The University of Michigan, Ann Arbor, Michigan, April 5, 1960.*

Black Rail in San Joaquin Valley of California.—On August 26, 1959, an adult male Black Rail (*Laterallus jamaicensis coturniculus*) was found dead near Fourteen Mile Slough, approximately four miles northwest of Stockton, San Joaquin County, California, by Mr. Paul Jorgensen. The bird was given to Dr. Kenneth Stocking of the College of the Pacific and the specimen was prepared as a skin by me (J. R. Arnold no. 881). Mr. Jorgensen reported to Dr. Stocking that a fence and other wires were present near where the bird was found. A broken wing was found at the time the skin was prepared. The only other record in this area known to me is that of Belding (Proc. U.S. Nat. Mus., 1, 1879:443).—JOHN R. ARNOLD, *Stockton College, Stockton, California, February 4, 1960.*

Insects Available for a Mockingbird Wing-flashing in February.—One of the prevalent theories concerning the enigmatic "wing-flashing" behavior of the Mockingbird (*Mimus polyglottos*) is that the wing motions flush insects to feed upon (see Hailman, Auk, 76, 1959:236–238 and references therein). It is known that wing-flashing occurs commonly in southern states but rarely in northern states during the winter (Sutton, Wilson Bull., 48, 1946:206–209; Tomkins, Wilson Bull., 62, 1950:41–42; Brackbill, Wilson Bull., 63, 1951:204–205; and Hailman, MS). It could be postulated that this is due to the unavailability of insects in the north during winter.

On February 28, 1960, my wife and I watched a Mockingbird wing-flashing on a grass roadway ten miles southeast of Norfolk, Virginia. Usually, wing-flashing is not seen in the Norfolk area until June. Many times after wing-flashing this bird pecked into the grass. It is of considerable interest to know whether or not moving insects were present where the bird was foraging and wing-flashing. A cursory search of a small area (six inches square) produced a small flea-like insect, an unidentified larva, a small burrowing insect, and a beetle. Thus, the association of wing-flashing with availability of potential prey is upheld.—JACK P. HAILMAN, *Bethesda, Maryland, February 29, 1960.*

Additional Data on the Establishment of the Chestnut-backed Chickadee at Berkeley, California.—A matter of interest concerned with the extension of geographic range of any species is the pattern of establishment after the initial invasion. The colonization of the Berkeley Hills of Alameda County, California, by the Chestnut-backed Chickadee (*Parus rufescens*) provides some information bearing on this point. In an earlier report (Condor, 56, 1954:113–124) I brought together available records outlining the progress of the colonization from 1938 through 1952. It appears that vegetational discontinuity in the area southeast of San Francisco Bay, acting as a barrier to the dispersal of an arboreal species, was bridged by the planting of orchards and shade trees, and, presumably following population build-up, the chickadees spread to occupy an area of favorable climate opposite the Golden Gate in the early 1940's. A number of reports indicate that the area occupied by this chickadee in the East Bay region has continued to expand: for example, Cogswell (Gull, 37, 1955:22) reported nesting at Mills College in Oakland in April, 1955, and Stallcup (Gull, 39, 1957: 10–13) listed the species from Alameda in December, 1956.

In the spring of 1959 I took advantage of limited opportunities to assess the current population levels of this chickadee along Strawberry Creek on the campus of the University of California in Berkeley, a locality at which this species was not known to nest prior to 1950. An equally important

objective was to determine the relative numbers and spatial relations of the chickadees and Plain Titmice (*Parus inornatus*) in view of the conclusion reached earlier (Dixon, *op. cit.*) that their breeding territories at this locality were mutually exclusive.

Even though the titmouse and chickadee share certain methods of food-seeking, one would expect them to be isolated ecologically since they differ in body size and bill form and the sites in the same trees where they concentrate their attention in foraging differ (Dixon, *op. cit.*). The conclusion that the chickadee takes numerous, smaller prey items is supported by the examination of the stomach contents of several titmice and a single adult chickadee taken on the same hillside, 3 miles east of

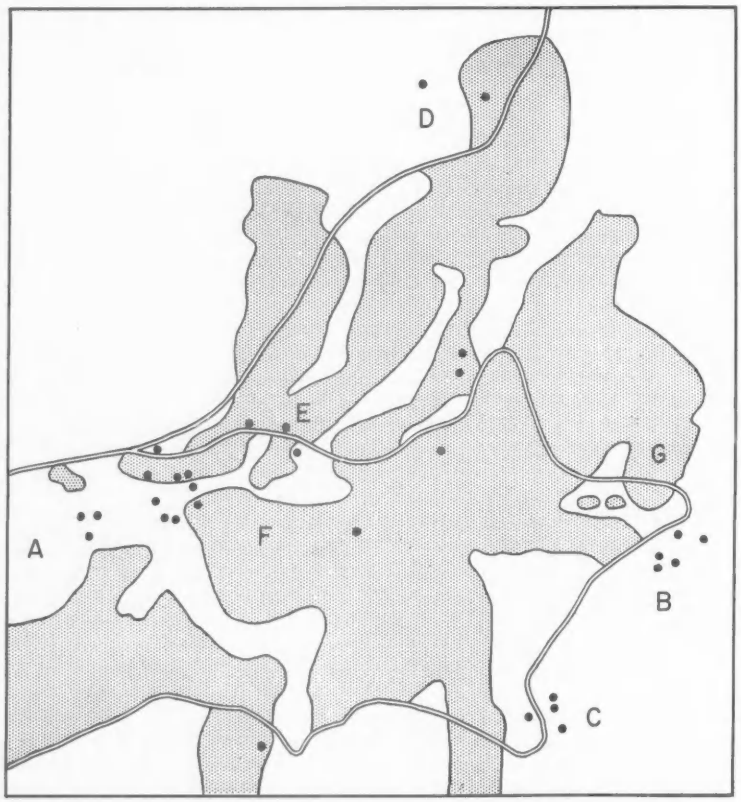

Fig. 1. Map showing where chickadees (A–D) were seen in 1959 in relation to distribution of live oak woodland (shaded). Plain Titmice centered at E, F, and G.

Jamesburg, Monterey County, California. The chickadee was obtained on May 29, 1959, while feeding fledglings in a mixed stand of oaks (*Quercus chrysolepis*, *Q. agrifolia* and *Q. lobata*) from which the titmice had been thinned earlier. The chickadee's stomach contained many aphids and other items smaller than those taken in any numbers by the larger congener. Conceivably this adult may have been feeding larger prey items to her offspring, but the fact that her stomach held approximately 100 aphids indicates that food items of this size are important in the diet.

Despite these dissimilarities in feeding, interspecific territorialism was witnessed at Berkeley in

1950, 1951 and 1952 (Dixon, *op. cit.*:121), and is judged to be important in the interactions of the two populations. The antagonism seems to be elicited by similarities in voice. Little information on territorial relations was gathered in 1959, although counter-singing was heard on February 19, and on April 4, I noted a titmouse in live oaks on a streambank supplant a chickadee repeatedly until the latter moved on.

Details concerning population levels will be presented separately for two sections of Strawberry Creek, namely, that portion traversing the University of California campus below the Memorial Stadium, and Strawberry Canyon proper above the stadium. Conditions for arboreal birds in the former area may be less favorable than they were 10 years ago as a result of the erection of new buildings on the campus. Except for a newly completed swimming pool, Strawberry Canyon is a relatively undisturbed area in which native vegetation predominates. No pronounced changes in vegetation over the past 12 years were evident to me other than increased stature of some trees on the north-facing slope and along the stream in the western part of the Botanic Garden and the notable increase in the extent of groves of redwoods west of the road in the northeast part of the study area mapped in 1948 (Dixon, Condor, 51, 1949:111).

Observations were made on the Lower Campus on February 19, April 3, 4, 6, 20 and 21, 1959, and in Strawberry Canyon on April 4, 5, 20, 21, and May 19. By early April the titmice were incubating, and territorial responses were infrequent. For this reason boundaries could not be delineated. Chestnut-backed Chickadees were not as far advanced in their nesting cycle, courtship feeding and a probable copulation being witnessed on April 5 and 4, respectively. However, the lack of a conspicuous "advertising" song in males of this species makes enumeration of breeding pairs difficult. Greater reliance is placed on records of chickadees prior to fledging since family groups tend to wander from the vicinity of the nest. However, records for early April are judged to represent breeding.

Lower Campus.—Chickadee activity was observed repeatedly in two separated parts of the glade between the Faculty Club and Stephen's Union and one pair of chickadees was noted west of the Life Sciences building. The first nestings occurred in the two areas in 1950 and 1952, respectively. These numbers represent no appreciable increase since 1952, although the presence in addition of three presumed pairs in an arc north and northeast of the Memorial Stadium in pines and eucalyptus indicates occupation of an area seldom utilized by Plain Titmice. (These latter chickadees are excluded from subsequent totals.) The presence of one pair of titmice in the Faculty Club glade between the chickadee pairs and two in the vicinity of the Life Sciences building in 1959 compares favorably with the situation of a decade ago.

Strawberry Canyon.—One pair of chickadees was detected on the north-facing slope in the vicinity of Plain Titmouse territory 16 of 1948 (see map, Condor, 58, 1956:170), and records for the eastern part of the study area as mapped represent three, and probably five, pairs. The accompanying map (fig. 1) indicates the points where chickadees were sighted in 1959 in relation to the distribution of live oak woodland. The records are clustered along the streamcourse to the west (A), in a madrone grove (B), along a willow-lined tributary (C), and in planted redwoods (D). I judged that three pairs of titmice were present in upland live oak groves of the same area, centered at points E, F, and G. There appeared to be four pairs of titmice in that part of the canyon below the Poultry Farm, but neither titmice nor chickadees were noted in the Poultry Farm area (titmouse territory 3 of 1947), a point verified by the further observations of William L. Thompson and Alden H. Miller. This area was occupied by titmice continuously from 1946 through 1952.

In the first 10 years of its occupancy of the Strawberry Creek area from the Botanic Garden to Oxford Street, the Chestnut-backed Chickadee has increased in population density from a single pair in 1950 (probably three pairs in 1952) to at least seven, and probably nine, pairs in 1959. The last level approximates that of the Plain Titmouse. The seven pairs of titmice in Strawberry Canyon proper in 1959 were equal to the average number for the period from 1947 to 1952 (Dixon, Condor, 56, 1954:121). Thus, the increase in numbers of the chickadee has not been achieved at the expense of the titmouse. By and large the activities of the two species are *centered* in different areas, most of the records of chickadees being in or adjacent to streamside growth of alders, willows, and shrubby dogwoods, or in planted conifers. It appears that the chickadees tend to accept as centers of nesting activity those sites that are not utilized extensively by the permanently territorial titmice. Chickadees are known to nest in oak woodland at Stanford University, California (Price, Condor, 38, 1936:24),

and titmice and chickadees may alternate in their occupancy of the same breeding territory in successive years (Dixon, *loc. cit.*). It appears that, as in the early 1950's, the chickadees avoid areas occupied by the titmice, and that space is not shared by the two species to an appreciable degree during the breeding season.

I am indebted to Paul D. Hurd, Jr., and Jack Powers for determination of the stomach contents reported here.—KEITH L. DIXON, *Hastings Natural History Reservation, University of California, Carmel Valley, California, December 30, 1959. (Present address: Department of Zoology, Utah State University, Logan, Utah.)*

Notes on Winter and Early Spring Bird Activity on the Farallon Islands, California.—Of the numerous published accounts of the birds of the Farallon Islands, few are based on observations made in the winter. Through the courtesy of the United States Coast Guard I spent several days, January 12 to 16 and March 17 to 23, 1960, on the Southeast Farallon Islands which are situated about 28 miles west of the Golden Gate Bridge, San Francisco, California. The primary purpose of my visit was to determine the winter activity of Cassin Auklets (*Ptychoramphus aleutica*). Each evening Cassin Auklets were noted coming in from the sea in large numbers about an hour and a half after sundown. In January no eggs were found, but the birds were active cleaning out old burrows. In some instances new burrows were begun in the soft soil, and many birds were engaged in mating activity. Burrows started on January 14 were incomplete; on March 18 they were approximately 30 inches in length. Mr. Ralph Gingles and Mr. Steven Brewster, resident Coast Guard personnel, informed me that the "night birds," as they call them, were first heard under the buildings during the last week of December of 1959 and that they returned in large numbers early in January. Their return in December coincides with the first heavy rain after the dry season. The rain appears to facilitate burrowing by dampening the soil. Dry soils cave in readily.

Upon arrival at the island the auklets immediately entered their burrows and began their subterranean activity. Between 10 and 11 p.m. most of the activity ceased and the auklets returned to sea. A few remained later, but by 2 a.m. the sounds of the auklets were rarely heard. This is in contrast to the full activity observed in March when the auklets demonstrated the greatest activity between midnight and dawn. On March 22 birds incubating eggs were present in approximately one-third of the nests examined.

In addition to this early nesting activity of the auklets in January, five Ashy Petrels (*Oceanodroma homochroa*) were found feeding young. All five young were fully feathered and almost ready to leave their nests in the rock walls. The young petrels were first discovered when I saw adults fly into a rock wall at about 9 p.m. on January 13; the feeding calls of the young were subsequently heard. This observation confirms the assumption made by Orr (Condor, 46, 1944:125–126) that the nesting of this species extends into mid-winter. On March 17, Ashy Petrels were numerous, occupying nesting holes, and were actively engaged in mating. This observation extends the breeding season to approximately 10 months on the Farallon Islands, or from about the middle of March to the middle of January.

In January numerous resident Rock Wrens (*Salpinctes obsoletus*), 10 to 12 Robins (*Turdus migratorius*), 7 Western Meadowlarks (*Sturnella neglecta*), 1 Red-shafted Flicker (*Colaptes cafer*), 1 Sparrow Hawk (*Falco sparverius*), 1 Belted Kingfisher (*Megaceryle alcyon*), and 2 Killdeers (*Charadrius vociferus*) were the conspicuous land birds noted. Recorded near the islands were flocks of Red-necked Grebes (*Podiceps grisegena*).—ASA C. THORESEN, *Department of Zoology, Oregon State College, Corvallis, Oregon, April 4, 1960.*

Confirmation of Occurrence of the American Redstart in Coastal Santa Barabara County, California.—Sight records of the American Redstart (*Setophaga ruticilla*) in coastal Santa Barbara County, California, on September 8, 12 and 16, 1957, have been published by the authors (Condor, 60, 1958:408). At this time, we wish to record a substantiating specimen, an immature male, taken in the same locality on September 25, 1959. The skin is deposited in the Santa Barbara Museum of Natural History (no. 4322).—CHARLES H. RICHARDSON and ALICE I. RICHARDSON, *Santa Barbara, California, April 15, 1960.*

Recent Records of the Little Owl and Water Rail in Korea.—On October 10, 1958, a dead Little Owl (*Athene noctua plumipes*) was given to me by one of the employees of the Army Post Exchange of Seoul, Korea. It was said to have been found in the folds of a tarpaulin on a supply truck that had arrived that morning from the port of Inchon on the Yellow Sea approximately 25 miles west of Seoul. Although the specimen was in good plumage, the body was in an emaciated condition and the stomach was empty. It weighed 108 grams. The sex was undetermined. According to Austin (Birds of Korea, 1948:149) only three records of this species exist for Korea, all based on specimens taken by Won in North Korea (Pyongan Namdo) in November, 1931, and February, 1932.

On January 28, 1960, Mr. Won Pyong Oh gave me a dead male Water Rail (*Rallus aquaticus indicus*) which he had purchased in the East Gate Market in Seoul the same day. According to Won, the shopkeeper claimed that it had been brought in from Chungchong Namdo, the province immediately south of and adjacent to Kyonggi-do, the province in which Seoul is located. The specimen was in excellent condition and weighed 129 grams. The stomach was empty. Austin, in reference to this species, states (1948:102), "From the specimen record it appears to be a rare transient" and lists a total of only eight specimen records for Korea, all taken in the months of November, October, and May. The present specimen appears to be the first definite winter record of the species in Korea.

Both specimens taken are deposited in the Museum of Vertebrate Zoology.—CHESTER M. FENNELL, *Seoul, Korea, February 3, 1960.*

Notes on the Behavior of the Xantus Hummingbird.—On November 7 and 8, 1959, under the sponsorship of the California Academy of Sciences and with financial support from the Belvedere Scientific Fund, Mrs. Wiggins and I were doing field work in the foothills of the Sierra de la Laguna between the village of Valle Perdido and Rancho la Junta, about 40 miles south of La Paz, Baja California. The region is one of rolling hills with general altitudes of 1200 to 1800 feet above sea level, and it is well clothed with semitropical scrub. In the canyons are two definite stories of vegetation. *Lysiloma candida, L. divaricata, Prosopis palmeri,* and an occasional tree of *Pithecellobium dulce* constitute the upper story and a number of different shrubs make up the lower one. On the adjacent slopes above the immediate influence of runoff in the bottoms of the canyons, *Cyrtocarpa edulis, Bursera microphylla, B. hindsiana,* and *Jatropha cinerea* comprise the upper story. Many of the perennials produce flowers during most of the year, and Xantus Hummingbirds (*Hylocharis xantusii*) are common residents.

About the middle of the afternoon of the 7th as I climbed toward the head of a small rock slide, a male Xantus Hummingbird flew in a close circle around my head. I "froze" and the hummingbird seemed to be merely curious; there was nothing belligerent about his actions. For the space of a trifle over three minutes he flew around my head, down to my feet, between my legs, up one side of my body and down the other, zig-zagged in front of my face, hovered, and circled. On four occasions as it made the circuits around my head the bird hovered directly in front of my face, tilted his head from side to side, approached more closely and touched the lenses of my glasses with the tip of its beak. It made no sounds that I could hear other than the slight whirring of its wings, nor did it touch my face or hands. The bird flew between my slightly straddled legs several times and ranged around my body in such a way as to give a very close inspection to every portion of my clothing and body. At the end of a final circuit around my head, it flew to a nearby twig of a *Lysiloma* tree and preened its wings and back for about twenty seconds, then flew rapidly up the hillside and out of sight.

Early the following day, as we camped beside a small stream flowing past Rancho La Junta, about two miles from the locality where the hummingbird had given me such a thorough inspection, another Xantus Hummingbird went through a similar routine around Mrs. Wiggins. This bird "ticked" the lenses of her glasses, and the fact that her lenses were heavily tinted, while those of my own were untinted, suggests that the contact was merely a tactile exploration and not an attempt to get at her eyes. This inspection lasted a shorter period than that of the previous afternoon, perhaps because I approached too closely and too rapidly, not knowing that a hummingbird was hovering in front of Mrs. Wiggins' face as I came up from down the canyon.

In the middle of the afternoon of the 8th I saw two Xantus Hummingbirds probing the flowers of *Ruellia peninsularis,* one of the shrubs frequently and regularly visited by this and other hummingbirds. Careful observation of their actions, and subsequent examination of the flowers they vis-

ited, revealed that they worked almost exclusively on buds that were nearly full grown but which had not yet expanded, their orifices tightly closed by the overlapping lobes of the funnelform corolla. The buds of this flower are about one and one-half inches long just before they open and have the five unequal lobes turned inward over the mouth in such a manner that the two forming the upper lip of the corolla are folded downward and inward at the tips; the central lobe of the lower lip turns abruptly upward outside of and over the notch between the two lobes of the upper lip. The two lateral lobes of the lower lip in turn overlap the edges of both the central lobe and those of the upper lip. Neat little pleats are folded inward into the throat of the bud at the angles between the margins of the upper and the lower lip. The whole chamber is thus effectively sealed against probing moths and other insects until the bud expands. The hummingbirds approached such large but unopened buds from a slight angle, and while hovering just barely to one side or the other of the tip of the bud, the bird would place the tip of its beak at the forward edge of one of the lateral lobes, give a slight but easily observed forward thrust and simultaneously execute a twist of the head so as to pry open the flap of tissue closing the bud at that point. With no appreciable delay the bird continued the thrusting motion and inserted its beak to the bottom of the bud where the nectar is secreted in this flower.

As soon as it was apparent that the hummingbirds went through this peculiar set of motions only in front of unopened buds, but inserted their beaks immediately into fully opened flowers, between twenty and thirty large but unexpanded buds were examined minutely, and a tiny opening at almost the same spot was found on each bud at which the hummingbirds had been observed. There seemed to be a slight preference for approaching the buds so as to open them from the right-hand side, as one faced the flower, but there were some that had been opened on the opposite side. The opening is made so skillfully that there is almost no tearing of the tissue of the flower's corolla, so the mechanical damage is insignificant.

We were in the field almost continuously from mid-October until late in December, and although hummingbirds of this and other species were observed visiting flowers belonging to a number of species, only the Xantus Hummingbird was observed probing unopened buds. Neither did we see the Xantus Hummingbird attempt to open unexpanded buds of any other species of plants.—Ira L. Wiggins, *Natural History Museum, Stanford University, Stanford, California, February 12, 1960.*

Records of Lewis Woodpecker for Humboldt County, California.—There are no records for the Lewis Woodpecker (*Asyndesmus lewis*) listed in Grinnell and Miller (Pac. Coast Avif. No. 27, 1944:1–608) for Humboldt County in northwestern California. From 1953 to 1960, I have three records for this county, all in October: one, Horse Mountain, October 10, 1954; one, near Sunny Brae, Arcata, October 1, 1958; three, flying several hundred feet above Klamath River at Orleans, October 5, 1958. The occurrence of this species in the inland mountainous country is to be expected, but the one seen near Arcata represents an unusual record. The latter area is in the redwood fog-belt for which there are no published records for the Lewis Woodpecker.—Charles F. Yocom, *Division of Natural Resources, Humboldt State College, Arcata, California, February 1, 1960.*

Immature Wood Duck, *Aix sponsa*, August 19, 1945, at Upper Thompson Lake, Lincoln County, Montana. Photograph by John L. Blackford.

NOTES AND NEWS

The Lida Scott Brown lectures in ornithology at the University of California, Los Angeles, in 1960 were presented by Dr. A. J. Marshall, Professor of Biology, Monash University, Victoria, Australia. The subjects of his four lectures on May 3, 12, 19 and 24 were: Birds of Australia and New Guinea; Birds of the High Arctic—Spitzbergen and Jan Mayen Land; Birds of Equatorial Africa—Lake Victoria; Birds of Islands and Deserts of Northwest Australia.

Recent significant literature received at the editor's desk has included the following:

"Comparative Breeding Behavior of Four Species of North American Herons" by Andrew J. Meyerriecks, Publications of the Nuttall Ornithological Club No. 2, 158 pages; this important monograph is made available by the Club at the excellent, low price of $3 per cloth bound copy as the result of a subsidy.

"A Field Guide to the Birds of Texas" by Roger Tory Peterson, $3.00; this is another fine and up-to-date unit in Peterson's series of guides.

"Proceedings, XII International Ornithological Congress, Helsinki, 1958," received August 9, 1960; 820 pages, in two paper-covered volumes. We understand that the main stock of the proceedings was destroyed by an accident following distribution of review copies but it is expected that a reissue of the work will be available soon.

ANNUAL BUSINESS MEETING OF THE COOPER ORNITHOLOGICAL SOCIETY, 1960

The first session of the annual meeting of the members of the Cooper Ornithological Society (a corporation) was called to order by President W. J. Sheffler in the Jean Delacour Auditorium, Los Angeles County Museum, Los Angeles, California, at 10:15 a.m., Friday, May 6, 1960.

The minutes of the meeting of 1959 were read and approved. The following committees were appointed: committee to examine proxies, James N. Bartel, Lillian K. Henningsen, Junea W. Kelly, chairman; committee on nominations, Jean Delacour, Gerhard Bakker, Jr., Joe T. Marshall, Jr., chairman.

Twelve proposals for membership were read (names and addresses in Secretary's files).

There being no further business, the meeting was adjourned until May 7.

The second session of the annual meeting of the members of the corporation was called to order by President W. J. Sheffler in Room 2147 Life Sciences Building, University of California, Los Angeles, California, at 9:20 a.m., Saturday, May 7, 1960.

Mrs. Junea W. Kelly, chairman of the committee to examine proxies, reported proxies for 872 members and over 25 members present in person. A quorum was declared present.

Dr. Joe T. Marshall, Jr., chairman of the committee on nominations, presented the following slate of nominees for the Board of Directors: Vernon Barrett, John Davis, C. V. Duff, Ed N. Harrison, Thomas R. Howell, Alden H. Miller, Frank A. Pitelka, W. J. Sheffler, and Jack C. von Bloeker, Jr. Junea W. Kelly moved that the nominations be closed and that the secretary cast an unanimous ballot for the slate of directors proposed by the committee on nominations. The motion was seconded and carried unanimously.

Dr. Alden H. Miller presented a resolution extending the thanks and sincere appreciation of the Society to the Local Committee under the chairmanship of Jean Delacour for the excellent arrangements which had been made for the annual meeting. The resolution was unanimously adopted.

C. V. Duff, Business Manager, presented his report. The Harry R. Painton bequest was received by the Society on August 20, 1959. This legacy, consisting of securities and cash, amounted to $61,128.07. At the close of business, December 31, 1959, the Society's securities totaled $178,623. In addition, there was $836.64 in cash awaiting investment. This represents a total increase over 1958 of $57,444.81. The endowment fund of $179,459.64 yielded an income of $5,240.66.

The following members took out Life Memberships in 1959: H. Lewis Batts, Jr.; John B. Davidson; S. H. French, III, M.D.; Ed N. Harrison, Jr.; J. R. Jehl, Jr.; S. Dillon Ripley; E. A. Schlesselman, M.D.; Paul A. Schwartz, Jr.; and Otis H. Wade.

The Society gratefully acknowledges generous gifts by Miss Isabel Thomson and John L. Blackford to the endowment fund.

There was an increase of 26 members in 1959, with a total membership of 1665.

There being no further business, the meeting stood adjourned.—JOHN DAVIS, *Secretary*.

For Sale, Exchange, and Want Column—Each member of the Cooper Society is entitled to one short advertising notice in any issue of the Condor free. Notices of over 3 lines will be charged for at the rate of 25 cents per line. Send advertising copy to Jack C. von Bloeker, Jr., Los Angeles City College, 855 N. Vermont Ave., Los Angeles 29, California.

FOR SALE—Magnemite 610E tape recorder modified and with accessories especially designed for bird song recording. Photographs and other information will be forwarded to serious inquirers.—WILLIAM R. FISH, *4532 Mill Race Rd., Sacramento 25, Calif.*

FOR SALE—"Field Record for Birds"—new type record book for yearly bird lists—40 pages, listing all birds of your area, plus 6 columns for information about birds. Makes an ideal annual list, 75¢ postpaid.—ERNEST S. BOOTH, *Box 1326, Escondido, Calif.*

SAVE $16.50 ON CHRISTMAS BINOCULAR SPECIAL—100% coated 7 × 35 center focus glass, with case, nationally advertised at $74.50 plus 10% tax, now until Christmas only $59.50 plus 10% tax. We are not permitted to use importer's name, but we can tell you each instrument has been checked and pre-serviced in our own Binocular Workshop and carries the MIRAKEL OWL guarantee that it is free of optical or mechanical defects and in alignment to 1/1000. Our catalog includes Bausch and Lomb, Grade A Bushnell Binoculars, and the budget-priced Mirakel Special line from $29.50 to $39.50 (plus 10% excise tax). Also, scopes from $54.50 to $115.00, each with built-in boss (for mounting scope directly on tripod) and shoulder strap, FREE to our customers. All instruments postpaid on 30-day trial; Christmas gifts on trial until January 10, 1961. (If ordered after December 1, 1960, request Special Handling shipment at our expense.) Send for catalog and copy of "Know Your Binoculars" reprinting our article published in Audubon Magazine, 10¢—no charge to COS members.—THE REICHERTS, *Mirakel Optical Co., Inc., 14 W. First St., Mount Vernon 15, N. Y.*

FOR SALE—Books on birds and natural history. Write for price list.—MRS. JOHN Q. BURCH, *4206 Halldale Ave., Los Angeles 62, Calif.*

WANTED—First class study skins of many species of Fringillidae and some other families; offer finely prepared specimens in exchange.—ALEX WALKER, *Tillamook County Pioneer Museum, 2106 Second St., Tillamook, Ore.*

FOR SALE—Write for complete details and specifications on Specimen Case no. 112, designed by the University of California. Size 27″ × 44″ × 42″—priced at $199.00, F.O.B. Escondido, Calif.—CHAPPELL'S HOUSE OF WOODCRAFT, *P. O. Box 105, Escondido, Calif.*

WANTED—Preserved avian specimens, just hatched, identified, maximum 12 hours old.—DAVID K. WETHERBEE, *307 Stockbridge Hall, Univ. Massachusetts, Amherst, Mass.*

FOR SALE—Eight original paintings of Australian parrots by the late Neville W. Cayley, 11″ × 15″—$45.00 each.—MARY P. HOPEGOOD, *116 Central Rd., Avalon Beach, N. S. W., Australia.*

WANTED—Needed to complete my COS file: Bull. Cooper Ornith. Club, vol. 1, nos. 3 and 4; The Condor, vol. 2, no. 6, and vol. 3, no. 2. Will buy any one, two, three, or all four items.—JACK C. VON BLOEKER, JR., *Los Angeles City College, 855 N. Vermont Ave., Los Angeles 29, Calif.*

PREPARATION OF MANUSCRIPTS FOR THE CONDOR

Articles published in the Condor normally are written by members of the Cooper Ornithological Society. Practically all the Society's money goes into the journal; neither the editor nor the business manager receives any pay other than the satisfaction of doing a service worthily. The preparation of good copy by the author will contribute greatly to accuracy of published output, dispatch in handling, and economy of production.

To be acceptable for inclusion in the Condor, articles should contain original material and indicate its significance. They must not duplicate in any substantial way material that is published elsewhere. Any type of subject bearing on birds will be considered. Manuscripts should be sent to the editor at the Museum of Vertebrate Zoology. Proofs with edited manuscripts will be sent to authors, at which time reprints may be ordered.

In the interests of accuracy and economy, observe the following: do not duplicate data in text, tables, or charts; check citations to original sources and verify text references; quoted statements must be exact replicas of the original; use vernacular names applicable to the entire avian species (for a guide in this regard, consult the A.O.U. Check-list of North American Birds, Fifth Edition, 1957; insert scientific names for species but not the subspecific name except in taxonomic papers or where the race concerned has been critically determined by the author or his collaborators on the basis of specimens; revise the manuscript repeatedly to remove superfluous words and phrases, immaterial detail, and repetitious statements.

Note Condor style and usage. "General Articles" and the "Field and Study" items are set up in different form. Provide a concise, meaningful title, and, where needed, subtitles within the text. Footnotes are not used. The address line may serve to indicate institutional connection, and to it should be added the date of transmittal of the manuscript. Terminal bibliographies are usually desirable where five or more titles are to be cited; otherwise, the references may be included in the text. For bibliographic style, note closely the practices employed in recent volumes of the journal. A factual summary is recommended for longer papers.

Rules for copy.—(1) Typewrite material, using one side of paper only; (2) double space all material and leave liberal margins; (3) use $8\frac{1}{2} \times 11$ inch paper of standard weight (avoid onion skin); (4) carbon copies are not acceptable; (5) place tables on separate pages and plan them to fit normal page width; (6) number pages in upper right hand corner.

Illustrations.—Photographs should be glossy prints of good contrast. Make line drawings with India ink; plan linework and lettering for at least $\frac{1}{2}$ reduction; do not use typewritten labels on the face of the drawing. Provide typed legends on separate sheets.

Helpful references on writing: Manual of Style, University of Chicago Press, and Rules of the Editorial Committee, University of California Press. On scientific nomenclature: Fifth Edition of the A.O.U. Check-list, The Distribution of the Birds of California (Pac. Coast Avif. No. 27), and The Distributional Check-list of the Birds of México, Parts I and II (Pac. Coast Avif. Nos. 29 and 33); authors are not required to follow the nomenclature of these works.